MORPHOLOGICAL VARIATION IN THE AVIAN PELVIS

by

Rachel A. Frigot

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Abstract

The hind-limb and its associated girdle perform a number of important functions in birds, including locomotion, feeding and reproduction. This has given rise to a number of efforts to correlate morphology of the hind-limbs to function, both to better understand the anatomy of living birds, and to infer the ecology of extinct ones. However, most of these studies have focused on the long bones of the hind-limb or have only considered narrow functional groups.

This thesis examines the pelvis of forty-two species of birds using three-dimensional geometric morphometrics, examining the morphology of six different hind-limb functional groups. Morphology is tested against body size and phylogenetic frameworks. A poor correlation is found between body size and morphology when Procrustes variables are regressed against species mass and against centroid size. Differences in morphology are found between functional groups, and pair-wise comparisons suggest that the pelvic morphology of carnivores is significantly different from all other functional groups, and that divers are significantly different from all other groups except paddlers. These relationships do not become less significant when phylogeny is taken into account and projecting phylogeny into shape space demonstrates extensive lability of pelvic morphology, suggesting that function has a greater influence over morphology than phylogeny. A brief exploration of sexual dimorphism shows that any shape differences between male and female individuals are, at best, a small contribution to total shape variation, and hint that sexually dimorphic shape changes might be restricted to smaller clades within birds. This agrees broadly with the morphological literature on bird

hind-limb morphology, and supports the use of morphology when making functional inferences about the hind-limb of extinct taxa.

Primary Reader: Adam D. Sylvester

Secondary Reader: Christopher Ruff

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Introduction

The crown clade Aves is a hugely diverse order (18,000+ species; Barrowclough et al., 2016) with a global distribution. Birds evolved from within maniraptoran theropods at some point in the Cretaceous (Huxley 1868, Gauthier 1986), though it is still being debated exactly which fossils are more closely related to birds than to other non-avialan therapods (Xu et al. 2011, Turner et al. 2012, Agnolin & Novas 2013, Godefroit et al. 2013, Brusatte et al. 2014). Accordingly, they demonstrate dinosaurian and theropod synapomorphies (Brusatte et al. 2014), with perforate acetabulae (Hutchinson 2001), reduced numbers of digits (Xu & Mackem 2013), and retroverted pubes (Hutchinson 2001). The origin of flight within, or outside of the group remains hotly contested (Dyke et al. 2013, Godefroit et al. 2013, Xu et al. 2015). The modern group has been able to diversify into a huge number of ecological roles and niches across all continents and oceans.

Prum et al. (2015) identify 14 major radiations within the modern clade of birds. Some of these, e.g., Falconiformes, are dominated by a shared major hindlimb function, in this case hunting and processing food (Ward et al. 2002, Struble & Organ 2016). Others, e.g., Charadriiformes, possess a number of locomotor styles (Strauch 1978, Prum et al. 2015). Most fundamentally, the clade is divided into two groups, the Paleognathae and the Neognathae (Prum et al. 2015). The paleognaths are restricted today to the ratites and tinamous, but several extinct groups existed (Davies & Bamford 2002). While they represent the largest living taxa, the locomotor modes that they represent are restricted as

all of the modern groups are terrestrial, with many being entirely flightless (Davies & Bamford 2002). Within paleognaths, only members of Tinamidae, the tinamous, retain the ability to fly (Davies & Bamford 2002). Today, the neognaths are far more speciose, representing the vast majority of extant bird taxa and ecological diversity (Prum et al. 2015).

Birds are active flyers, and accordingly possess several adaptations to deal with the problems posed by flight: pneumatised skeletons allowing increased bone stiffness without increasing mass (Currey & Alexander 1985), strut-like trabeculae (Rogers & LaBarbera 1993) and, fused regions of the vertebral column (Baumel 1993). The flight surface of birds is generated by the feathers of the wing. The leading edge is extended by the primary feathers and the aerofoil cross-section is defined by the packing of the covert feathers. The wing is stiffened chordwise by the rachis of the feathers and so needs no trailing edge support (Rayner 1988). As a result, the hindlimb is not required to contribute to the wing and so allows birds to have separate locomotor modules, with the hindlimbs dedicated to non-volant locomotion and the wings to flight (Gatesy & Dial 1996).

As a highly speciose and globally ranging clade, birds show high morphological and ecological disparity. Avian ecology and its role in the acquisition of flight have been areas of scientific interest (Padian & Chiappe 1998, Hedenström 2002, Dececchi & Larson 2011, Brusatte et al. 2015) since the description of *Archaeopteryx* (Owen 1863), and many recent studies have used bird function to attempt to reconstruct the evolution of

flight (Dial 2003), to hypothesize the pre-flight function of feathers (Clarke 2013), or to reconstruct the function of extinct stem or crown birds (Palmqvist & Vizcaíno 2003). Many existing studies of avian limb allometry attempt to address questions in this last category, either to develop datasets for reconstruction of wing variables from single bones (Nudds 2007), to constrain flight capabilities (Vizcaíno & Fariña 1999, Chatterjee et al. 2007), or to attempt to categorise ecology of extinct taxa (Bell & Chiappe 2011). Avian body size has been shown to have consequences for clutch size (Price & Liou, 1989), brain size (Iwaniuk et al. 2004), and energy expenditure (McNab, 1994).

The large disparity in avian ecological traits has naturally attracted much research attention towards understanding morphological adaptation for function (Rayner 1988, Marsh & Dawson 1989, Worthington 1989, Hedenström 2002, Winger & Bates 2015, Zhang et al. 2016), often with an eye to conservation of species (Green et al, 1989, Garcia et al. 2017, Murgui & Hedblom 2017). Among these adaptational studies, a number seek to find relationships between osteology and ecology, often for reconstruction of extinct ecologies (Hinić-Frlog & Motani 2010, Bell & Chiappe 2011, Field et al. 2013, Bell et al. 2019). Several studies (Warham 1977, Mönkkönen 1995, Hertel & Ballance 1999, Bell & Chiappe, 2011, Zeffer et al. 2003, Hinić-Frlog & Motani, 2010, Stoessel et al. 2013) have established that avian ecology has an effect on the morphology of the limb skeleton, with many (Zeffer et al. 2003, Reynaud 2006, Hertel et al. 2007, Endo et al. 2012, Stoessel et al. 2013, Bell et al. 2019) focussing on the pelvic limb. This limb is less involved in flight than the fore-limb, but has functions in reproduction (Dyke & Kaiser 2010) and non-aerial locomotion.

The pelvis of birds demonstrates a tendency to recruit vertebrae from both the dorsal and caudal segments of the spine into a complex synsacrum. They are fused, with ilia extended both anteriorly and posteriorly, and strongly retroverted pubes (Iijima & Kobayashi 2014). The bird femur has a trochanter and medially directed head (Baumel 1993), and sits inside a perforate acetabulum (Hutchinson 2001). The pelvis is ventrally open, lacking midline symphyses (Baumel 1993, Dyke & Kaiser 2010). It is not well understood which of these pelvic features are related to flight, and which to other characteristics, such as oviparity. The avian pelvis has long been believed to differ in shape between males and females due to the need for females to lay eggs (Dyke & Kaiser 2010), with egg shape correlating to pelvic shape (Shatkovska et al. 2018). It is known that at least some taxa show sexual dimorphism in body size, and that this frequently relates to reproductive strategy (Szekely et al. 2007).

Despite being such an active area of research, morphological research on the hindlimb of birds has largely focussed on the long bones of the limb (Maloiy et al. 1979, Gatesy & Biewener 1991, Barbosa 1993, Barbosa 1999, Christiansen 1999a, Nemeschkal 1999, Dyke & Nudds 2009, Dececchi & Larson 2011, Doube et al. 2012, Dececchi & Larson 2013, Killbourne 2013, Bell et al. 2019), a number of studies track the pathway from non-avialan dinosaurs to modern birds (Gatesy 1991, Dececchi & Larson 2011, Dececchi & Larson 2013), looking at relative proportions of the limbs in order to investigate the evolution of flight, or to address the dichotomy between the “trees down” or “ground up”

models of flight acquisition (Padian & Chiappe 1998, Dececchi & Larson 2011). Some examine living birds in order to infer ecology of extinct ones (Dyke & Nudds 2009, Bell & Chiappe 2011). Other papers look primarily at living birds, to relate hindlimb morphology to ecology (Barbosa 1993, Barbosa 1999, Doube et al. 2011, Bell et al. 2019).

Of these, Doube et al. (2012), Maloiy et al. (1979) and Gatesy & Biewener (1991) analyse the skeleton from a mechanical perspective. Doube et al. (2012) test the long-held belief that bird skeletons are "light" due to their increase in intracortical space and pneumatisation and examine how the limb bones scale with body mass. They find that the femora are isometric in length as mass increases, but that the tibiotarsus and tarsometatarsus are positively allometric in length. This may suggest that their larger flightless birds (e.g. ostriches) have longer limbs as an adaptation to cursoriality, rather than in response to increased mass *per se*. Maximum second moments of area of all three of the long bones are also found to be positively allometric as body mass increases, increasing the rigidity of the long bones. This is very similar to the approach previously taken by Maloiy et al. (1979), although they examine only running in terrestrial birds, and find that the bones appear to better fit the elastic similarity model proposed by McMahon (1973). Gatesy & Biewener (1991) tackle allometry of the limb bones in a different manner, looking instead at gait and stance changes as body mass increases. They find that, similarly to the case in mammals (Biewener 1989), more massive birds have a more upright stance, and that this remains the case regardless of gait utilised.

By contrast, relatively few studies (Hertel et al. 2007, Ibáñez & Tambussi 2012, Anten-Housten et al. 2017) focus on the pelvic girdle itself. This is likely a result of the complexity of the pelvis when compared to the rest of the bones of the hind-limb. Only Ibáñez & Tambussi (2012) attempt to utilise geometric morphometrics to address this complexity, and they do so using two-dimensional images, on a relatively constrained group of taxa. The work presented here aims to increase the taxonomic breadth and functional disparity over which pelvic morphology is analysed, by addressing several interrelated questions:

1) Do birds demonstrate variation in pelvic shape related to hindlimb function?
Birds are known to have different locomotor strategies, and display numerous adaptations to their lifestyles. It would be expected that, along with other skeletal adaptions, the shape of the pelvis would change to allow efficient use of the hindlimb in the positions and behaviours habitually utilised by that species.

Hypothesis 1: Birds will exhibit significant clustering in morphospace between hindlimb functional groups.

2) Are functional shape changes present independent of body size?
Body size and the problems of scale have been repeatedly demonstrated in mammals to have an effect on both skeletal architecture and on the stance utilised (Alexander et al. 1979, Biewener 1983, Biewener 1989, Biewener 1990, Christiansen 1999b). Larger animals have more robust skeletons, with longer processes and greater mechanical

efficiency, but they also utilise more graviportal stances, with the limbs straighter (Biewener 1989, Gatesy & Biewener 1991). Together, these adaptations reduce stress on the skeleton (Doube et al. 2012). They also introduce a confounding effect between hindlimb use and body size, which needs specific testing.

Hypothesis 2: Some aspects of pelvic shape change will be better explained by body size than hindlimb function.

3) Are functional shape changes independent of phylogenetic relatedness?

In a similar manner to body size, shared shape change through common descent can act to confound any functional signal in pelvic shape. In this case, it would be expected that more closely related species would have more similar pelvic shape, as the timespan over which variation accrued from the last common ancestor was shorter. If two closely related species have differing hindlimb functions and pelvic morphology is not highly responsive to function, it may then be expected that evolution has not had sufficient time to optimise the pelvis from the ancestral condition. They may therefore remain more similar to each other than to more distantly related taxa with similar hindlimb function. This would be tested for by shape comparison within an explicit phylogenetic model, assuming that only evolution since the last common ancestor could be considered truly independent.

Hypothesis 3: When phylogenetic relationships are accounted for, hindlimb functional groups will remain more similar than phylogenetic groups.

Materials and Methods

A taxonomic sample of extant avian species was selected to allow good taxonomic spread and sampling within the avian clade, in conjunction with the large genetic phylogeny produced by Prum et al. (2015) and the holdings of the Smithsonian Museum of Natural History Bird Division (NMNH). Prum et al. (2015) was chosen for the phylogenetic model in this work due to its use of genetic characters to reconstruct phylogenetic relationships. This maximises independence between the characters used for the phylogenetic reconstruction and the characters analysed using that phylogenetic model, preventing circularity. Further, Prum et al. (2015) was chosen due to the large taxonomic sample and large genetic dataset of characters. Taxa were selected from within the phylogeny to represent a diversity of locomotor habits, body sizes and sub-clades, with at least two taxa being selected from each subclade, wherever possible. In some cases, substitutions were made with other taxa of the same genus or family to maximise the museum holdings of the species selected in the hope of having adequate suitable specimens for analysis. In the cases of con-familial substitutions, taxa were inserted into the Prum et al. (2015) phylogeny based upon smaller, family or order level phylogenetic analyses, again using data from genetic phylogenies wherever possible. The studies used for each taxon are shown in Table 1. A few taxa were added to the phylogeny in a similar manner in order to capture taxa with differing hindlimb functions, for instance. Individual specimens included in the study are given in Appendix 1.

Hindlimb functions were defined according to the primary feeding and non-aerial locomotor strategies, similar to those of Chiappe & Bell (2011). These habits were gathered from lay scientific publications on bird habits, and can be seen in Table 1. Carnivores were defined as species that hunt or scavenge prey and process it with assistance of the hind-limb. Climbers were defined as species that utilise arboreal resources other than solely the branch, or that feed extensively within trees. This may be further indicated by the presence of crevice nesting. Divers are aquatic species that swim extensively under the surface of the water, while paddlers remain principally upon the surface, although they may dabble. Perchers are arboreally dwelling taxa that do not extensively locomote within trees, tending instead to fly between tree and ground, or tree to tree. This term is used instead of "perching" to prevent confusion between this locomotor habit and the Passeriformes, which are commonly known as "perching birds". Walkers are species that principally dwell and feed upon the ground, or wade. They may or may not be capable of flight.

Where possible, a sample of two male and two female specimens were selected for each taxon. Only complete, adult specimens without visual deformation were chosen. Adult specimens were defined based upon a complete closure of the sacro-iliac suture. In some instances, fewer specimens were available, but the taxon was included anyway in order to maintain taxonomic, functional or body size diversity. Sample sizes are indicated in Table 1.

Taxon	N(♀/♂)	Nearest relation in Prum et al. (2015)	Shared level	Family	Order	Mass (g)	Hindlimb function
Accipiter gentilis	4(2/2)	*Accipiter superciliosus*	Genus	**Accipitridae**	Accipitriformes	1089 /749	Carnivore
Ara chloropterus	4(2/2)	*Deroptyus*	Family	**Psittacidae**	Psittaciformes	1214	Climber
Arenaria interpres	4(2/2)	-	-	**Scolopacidae**	Aequorlitornithes	138/134	Walker
Cathartes aura	4(2/2)	*Cathartes burrovianus*	Genus	**Cathartidae**	Accipitriformes	1611	Carnivore
Chauna torquata	4(2/2)	-	-	**Anhimidae**	Anseriformes	4400	Walker
Choriotis kori	4(2/2)	-	-	**Otididae**	Otidimorpha	5635/11281	Walker
Ciconia Ciconia	4(2/2)	*Ciconia nigra*	Genus	**Ciconiidae**	Aequorlitornithes	3325/3571	Walker
Climacteris leucophaea	1(-/1)	*Climacteris melanura*	Genus	**Climacteridae**	Passeriformes	22	Climber
Colaptes auratus	4(2/2)	*Picus*	Family	**Picidae**	Coraciimorphae	125/128	Climber
Colius striatus	4(2/2)	*Colius colius/Colius indicus*	Genus	**Coliidae**	Coraciimorphae	51.1	Percher
Columbina passerina	4(2/2)	*Columbina minuta*	Genus	**Columbidae**	Columbimorphae	33.4	Percher
Cuculus canorum	4(2/2)	*Cuculus optatus*	Genus	**Cuculidae**	Otidimorpha	106/117	Percher
Eclectus roratus	1(1/-)	*Barnadius*	Family	**Psittacidae**	Psittaciformes	561	Percher
Eudromia elegans	4(2/2)	-	-	**Tinamidae**	Tinamiformes	729/678	Walker
Eurypyga helias	4(2/2)	-	-	**Eurypygidae**	Aequorlitornithes	210	Walker
Falco peregrinus	4(2/2)	*Falco sparverius*	Genus	**Falconidae**	Falconiformes	873/649	Carnivore
Francolinus capensis	3(1/2)	*Numida*	Family	**Phasianidae**	Galliformes	547/758	Walker
Furnarius leucopus	4(2/2)	*Furnarius rufus*	Genus	**Furnariidae**	Passeriformes	54.8	Percher
Gallinula chloropus	4(2/2)	*Porphyrio porphyrio*	Family	**Callide**	Gruiformes	294/359	Paddler
Gavia immer	4(2/2)	-	-	**Gaviidae**	Aequorlitornithes	4500/5640	Diver
Geococcyx californianus	4(2/2)	Sister to cuckoos excluding *Centropus*	Family	**Cuculidae**	Otidimorpha	376	Walker
Grus canadensis	4(2/2)	-	-	**Gruidae**	Gruiformes	4096/4848	Walker
Larus argentatus	4(2/2)	*Chroicocephalus cirrocephalus*	Family	**Laridae**	Aequorlitornithes	1022/1150	Paddler
Meleagris gallopavo	2(1/1)	*Gallus gallus*	Family	**Phasianidae**	Galliformes	4300/7800	Walker

Oceanodroma leucorhoa	4(2/2)	-	-	**Hydrobatidae**	Aequorlitornithes	37	Paddler
Opisthocomus hoatzin	2(1/1)	-	-	**Opisthocomidae**	Opisthocomiiformes	696	Climber
Pelecanus occidentalis	4(2/2)	-	-	**Pelecanidae**	Aequorlitornithes	3174/3702	Diver
Phaethon rubricauda	4(2/2)	-	-	**Phaethontidae**	Aequorlitornithes	675	Diver
Phalacrocorax auritus	4(2/2)	*Phalacrocorax brasilianus*	Genus	**Phalacrocoracidae**	Aequorlitornithes	1808/2077	Diver
Phoenicopterus ruber	4(2/2)	-	-	**Phoenicopteridae**	Aequorlitornithes	2573/3529	Walker
Podiceps grisegena	4(2/2)	*Rollandia rolland*	Family	**Podicipedidae**	Aequorlitornithes	1023	Diver
Pterocles decoratus	3(1/2)	*Pterocles bicinctus*	Genus	**Pteroclididae**	Columbimorphae	180/188	Walker
Ptilonorhynchus violaceus	4(2/2)	-	-	**Ptilonorhynchidae**	Passeriformes	213/225	Percher
Ramphastos sulfuratus	4(2/2)	*Ramphastos ambiguus*	Genus	**Ramphastidae**	Coraciimorphae	389/430	Climber
Somateria mollissima	4(2/2)	*Aythya valisineria*	Family	**Anatidae**	Anseriformes	1915/2218	Paddler
Tauraco corythaix	2(2/-)	*Tauraco macrorhynchus*	Genus	**Musophagidae**	Otidimorpha	308	Percher
Threskiornis aethiopicus	4(2/2)	*Theristicus caerulescens*	Family	**Threskiornithidae**	Aequorlitornithes	1378/1618	Walker
Trichoglossus haematodus	4(2/2)	*Barnadius*	Family	**Psittacidae**	Psittaciformes	95/102	Percher
Turnix suscitator	1(1/-)	*Turnix ocellatus*	Genus	**Turnicidae**	Aequorlitornithes	57.5	Walker
Tyto alba	4(2/2)	-	-	**Tytonidae**	Strigiformes	419/362	Carnivore
Upapa epops	4(2/2)	-	-	**Upupidae**	Coraciimorphae	61.4	Percher
Xiphorhynchus guttatus	4(2/2)	*Furnarius rufus*	Infraorder	**Dendrocolaptidae**	Passeriformes	59.8	Climber

Table 1: Details of taxa used for the analysis. Additionally, the attributes assigned for further analysis, including relationship to closest related taxon in Prum et al. (2015), mass and hindlimb functional group.

Selected specimens were three-dimensionally surface scanned using 360° scans in at least two orthogonal axes using a NextEngine surface scanner. Macro view was used whenever the specimen would fit within the available field of view, with wide view used for the remainder. Twelve divisions were used for each scan, and high-resolution scans (29 thousand dpi) were made. The resulting scans were cropped and aligned using ScanStudio (Santa Monica, 2000) software before being exported as PLY files. Three-dimensional landmarks were applied using Landmark.exe (Wiley et al., 2007) and imported as an NTS file into RStudio (version 1.1.463; RStudio Team 2016) running R (version 3.5.2; R Core Team 2018). One hundred and ten landmarks were placed, with 22 fixed full landmarks (Bookstein 1986, 1997) and the remaining 88 landmarks later allowed to slide (Rohlf & Slice 1990) as semi-landmarks (Figure 1, Table 2). The semi-landmarks were placed at a density approximately inverse to the curvature at each point. These curves were resampled in R to give equal spacing along the curve, prior to any further analysis. During the resample, the number of semi-landmarks in each curve was reduced by two, giving a total of 86 landmarks for analysis, of which 64 were semi-landmarks, describing 12 curves.

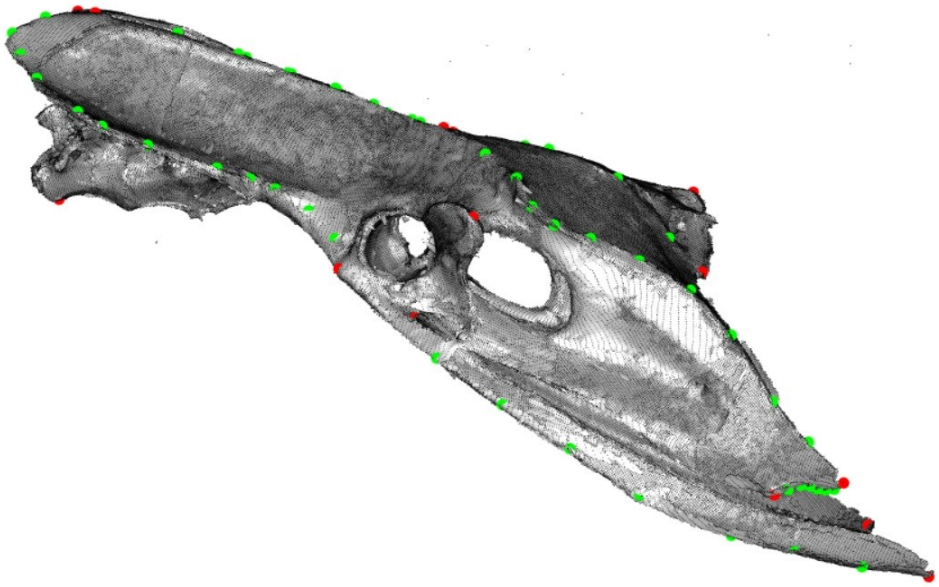
During the analysis in R using package "geomorph" (Adams & Otarola-Castillo, 2013, Adams et al. 2018), an initial partial Procrustes analysis (Zelditch et al. 2012) was performed with all 110 landmarks and no semi-landmark sliding, in order to collect the centroid size for each specimen, prior to alteration or scaling during subsequent analysis. Following this, to ensure symmetrical data and minimise the effects of any post-mortem deformation, the curves were resampled and each specimen was then reflected

mathematically, and a partial Procrustes analysis was performed on the mirrored configurations to fit them, and the average of the points was taken and as a symmetrical configuration for further analysis. At this point, the semi-landmarks were not permitted to slide, in order to prevent repeated sliding causing landmarks to move from the surface (Gunz & Mitteroecker 2013). Alignment according to principal axes was not permitted, in order to prevent difficulties arising from mirroring in this R package, a bug that had not been fixed as reported (Adams 2018).

A further partial Procrustes analysis was then performed across all specimens (Rohlf & Slice 1990, Zelditch et al. 2012, Adams et al. 2018), in which the semi-landmarks were permitted to slide in order to minimise Procrustes distance and in which alignment according to principal axes was not permitted. The reference specimen was the F1 specimen of *Accipiter gentilis*, and iterations of fit were not restricted and allowed to run to completion. The Procrustes co-ordinates from this analysis were used in subsequent analyses.

A Procrustes regression was performed (ProcD.lm), using ANOVA to look for covariance of Procrustes shape variables against logarithmically transformed body mass and against logarithmically transformed centroid size in order to test for fit of shape against a linear variable (Adams & Collyer 2018). Body mass estimates were obtained from Dunning (2007). Species mean values were used in order to apply a consistent method across all taxa, as body mass records were not present for all of the specimens scanned.

A



B

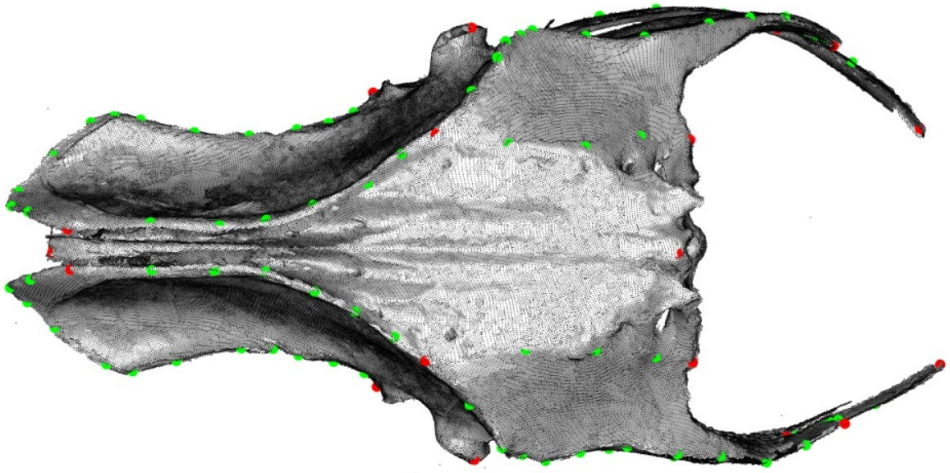


Figure 1: Placement of landmarks. Surface scan of *Choriotis kori* in left lateral (A) and dorsal (B) views, demonstrating the placement of landmarks on the surface. Landmarks coloured red were full landmarks, while landmarks coloured green were resampled as curves and used as sliding semi-landmarks. Definitions of each landmark can be found in Table 2.

Landmark number	Location
1	Cranial extent of dorsal median ridge
2	Caudal extent of dorsal median ridge
3	Ventral-most point of cranial surface of the body of the first synsacral vertebra
4	Ventral-most point of caudal surface of the body of the last synsacral vertebra
5 & 6	Cranial end of sacro-iliac suture on left and right sides, respectively
7 & 8	Intersection of crista terminale and sacroiliac suture on left and right sides, respectively
9 & 10	Caudal extent of sacro-iliac suture on left and right sides, respectively
11 & 12	Caudal extent of crista terminale on left and right sides, respectively
13 & 14	Pectinate process on left and right sides, respectively
15 & 16	Antitrochanter on left and right sides, respectively
17 & 18	Cranial most point of obturator foramen on left and right sides, respectively
19 & 20	Ventro-caudal extent of ischium on left and right sides, respectively.
21 & 22	Caudal extreme of pubis on left and right sides, respectively.
23 – 33 & 34 – 45	Lateral margin of preacetabular process on left and right sides, respectively.
46 – 51 & 52 – 57	Sacro-iliac suture along preacetabular process on left and right sides, respectively.
58 – 60 & 61 – 63	Sacroiliac suture posterior to crista terminale on left and right sides, respectively.
64 – 73 & 74 – 83	Crista terminale (ilioischial suture) on left and right sides, respectively.
84 – 89 & 90 – 95	Caudal margin on ischium on left and right sides, respectively.
96 – 102 & 103 – 109	Ventral margin of pubis on left and right sides, respectively.

Table 2 – Definitions of landmarks and curves defined by landmarks. All curves were defined by placing landmarks in order from cranial to caudal, except for 84 – 89 & 90 – 95, in which landmarks were placed from medial to lateral.

Further, it is far from certain that the body mass at time of death would represent a normal, healthy body mass for that individual. Where multiple subspecies were present, these were pooled using a weighted mean. Separate means for males and females were

used where available. The regressions performed against logarithmically transformed centroid size allowed for a more individual analysis of pelvic size and shape.

Morphological sexual dimorphism was tested in this dataset using a between-groups principal components analysis (BG-PCA; Mitteroecker & Bookstein 2011) on the Procrustes co-ordinates of taxa where the number of males and females was equal (36 taxa, 140 specimens). All female specimens were treated as a single group, and all male specimens as another. The purpose of this was to maximise the distance between the mean female and mean male configuration in shape space. Sexual size dimorphism was tested using a one-way ANOVA for centroid size using sex as a grouping criterion. Mass was not used in this last analysis, due to the lack of specimen-specific data available. For visualisation purposes, a principal components analysis was carried out using all specimens.

For the phylogenetic analyses, node divergence dates were taken from Prum et al. (2015), with the taxonomic subsampling being sufficiently small that there were no equivocal sister group relationships. Two nodes were of uncertain date, both leading only to terminal branches of the tree (*Trichoglossus* + *Eclectus* and *Furnarius* + *Xiphorhynchus*). Both were bounded by nodes in Prum et al. (2015) such that a maximum divergence time could be established. In these instances, the midpoint between the prior node and the present day was calculated and the later divergence point was chosen between this midpoint and the maximum divergence.

The phylogenetic tree discussed above was combined with node divergence dates that were also taken from Prum et al. (2015), with the taxonomic subsampling being sufficiently small that there were no equivocal sister group relationships. Two nodes were of uncertain date, both leading only to terminal branches of the tree (*Trichoglossus* + *Eclectus* and *Furnarius* + *Xiphorhynchus*). Both were bounded by nodes in Prum et al. (2015) such that a maximum divergence time could be established. In these instances, the midpoint between the prior node and the present day was calculated and the later divergence point was chosen between this midpoint and the maximum divergence. The resulting phylogeny contains 42 taxa and is shown in Figure 2.

To test for functional effect, PC scores of all specimens in a species were averaged to (Jorgensen & Reilly 2013) and were tested using multiple analysis of variance (MANOVA) across the principal components that accounted for 95% of shape variance, in both a non-phylogenetic and phylogenetic context. Phylogenetic analyses were performed using the "phytools" package (Revell 2012). The PC scores averaging was made necessary by the R functions in use, as they do not allow nested variables, or variables represented by more than one number (e.g. *x*, *y* and *z* co-ordinates).

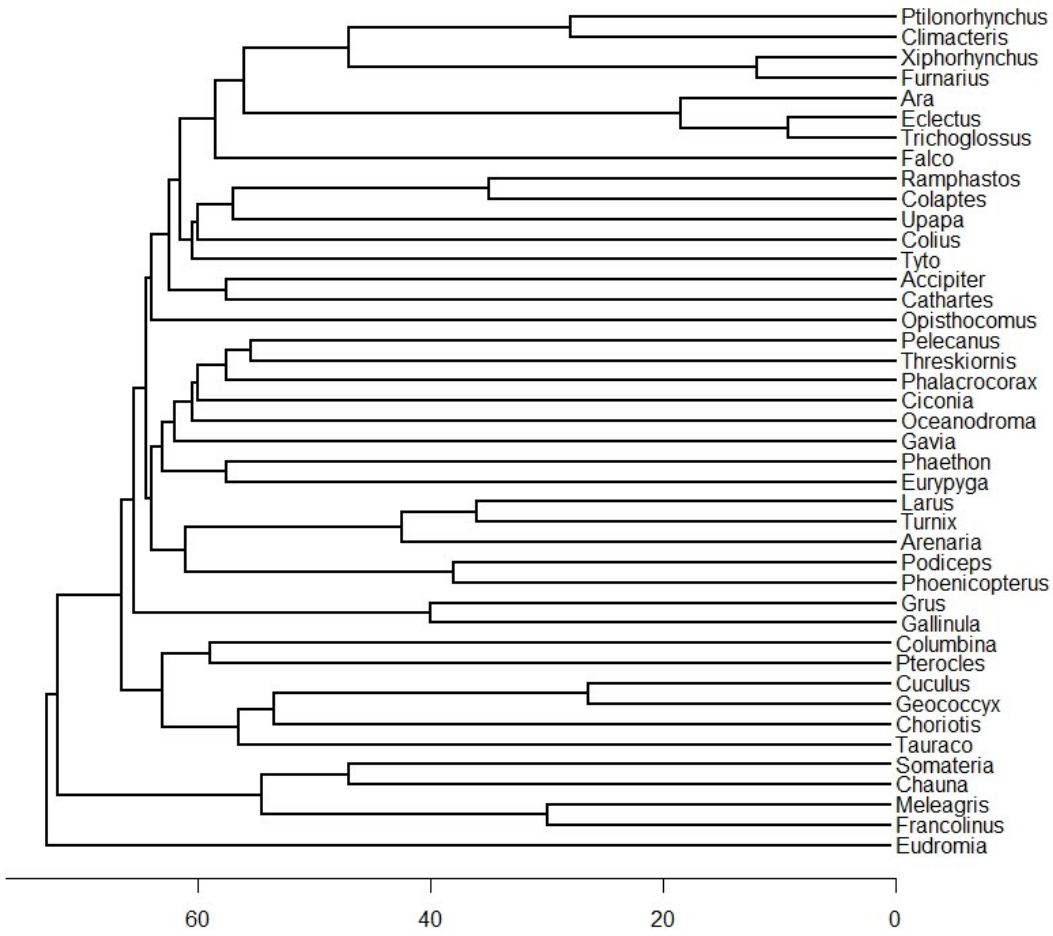


Figure 2: Scaled phylogenetic tree modified from Prum et al. (2015). Axis shows time in millions of years (mya).

First, the specimen level PC scores were analysed across the first 26 PCs using a nested MANOVA, testing for differences between the defined functional groups. Nesting was based upon the taxonomic groupings in the analysis, using genus as an error term. The data were further analysed using a phylogenetic MANOVA (pMANOVA) to explicitly address the non-independence of related taxa and the expected similarity in shapes as a result of phylogenetic constraint.

In order to assess which functional groups might significantly differ from each other, pairwise one-way Hotteling's T^2 test were performed across functional groups of specimens, utilising the first 26 PCs (95% of shape variance) between each group, in order to identify which groups had significantly different means. Significance was set at 0.0033 following a Bonferroni adjustment taking into account the number of pairwise comparisons between functional groups (fifteen).

Results

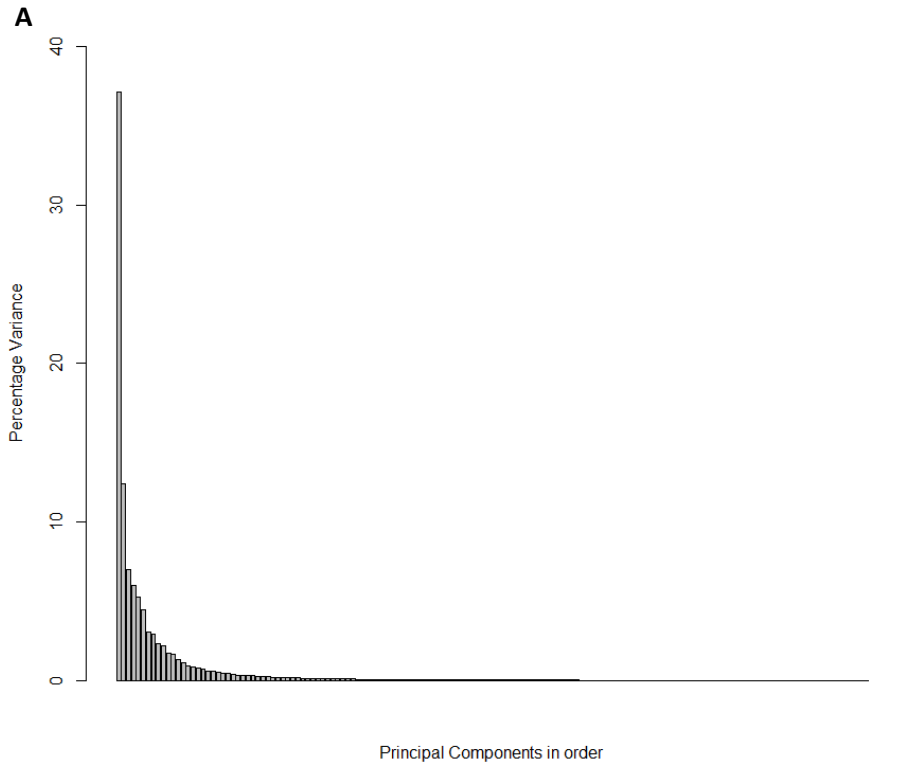
The first 26 PCs were required to account for 95% of the shape variation in the avian taxa, with PC1 accounting for 37%, PC2 accounting for 12% and PC26 accounting for 0.3%. A summary of the variances can be seen in Figure 3A. Figure 3B shows the PC1 and PC2 scores of all specimens, showing that at least two groups of specimens appear to exist in morphospace without highlighting functional groupings.

For brevity, the configurations of the maximum and minimum ends of the PC axes for the first six PCs can be seen in Figure 4. These are displayed as they represent the PCs before a visible drop in the amount of variance accounted for by subsequent PCs (Figure 3A), although the PCs that cumulatively accounted for 95% of variance are used for analysis. As can be seen, PC1 is largely descriptive of the overall aspect ratio of the pelvis, with elongate pelves scoring more negatively, and more equant ones scoring more positively. PC2 seems to reflect the contributions to dorsal surface area by the synsacrum, ilium and ischium.

The Procrustes regressions showed that both centroid size (R^2= 0.16, p=0.001) and mass (R^2= 0.085, p=0.001) were correlated to specimen shape (Figure 5A & B, respectively). These results were highly significant, but with very low R^2 values showing a low predictive power between size and shape. Due to the extremely low correlation scores, body size was not considered in subsequent analyses. The maximum shape shows that, on average, large pelves are slightly more elongate, and small pelves are slightly more equant (Figure 5C & D), but there was a high degree of variability from the trend.

In the BG-PCA for sexual dimorphism, there was no significant difference in shape between the sexes across birds as a whole (Figure 6), with the between-group axis explaining 100% of shape variation. When visualised on the PC1 and PC2 plot (Figure 7), it can be seen that sexual dimorphism may be suggested in some taxa, but any consistent differences between the sexes are contributing at most only a small amount to total shape variance and as such are likely to be obscured by variation among taxa. Between sex shape changes can therefore only be seen in instances where shape differences between sexes are considered as an *a priori* assumption. The one-way ANOVA testing effect of sex on centroid size was non-significant, (F = 1.024, p = 0.31).

When a phylogenetic tree is superimposed upon the PC scores (Figure 8), it looks as though the phylogenetic history of the avian pelvis does not appear to have a strong influence upon the shape of the pelvis, something further supported by the phylogenetic and non-phylogenetic MANOVA, which show a near identical p-value regardless of whether or not phylogeny is taken into account (Table 3).



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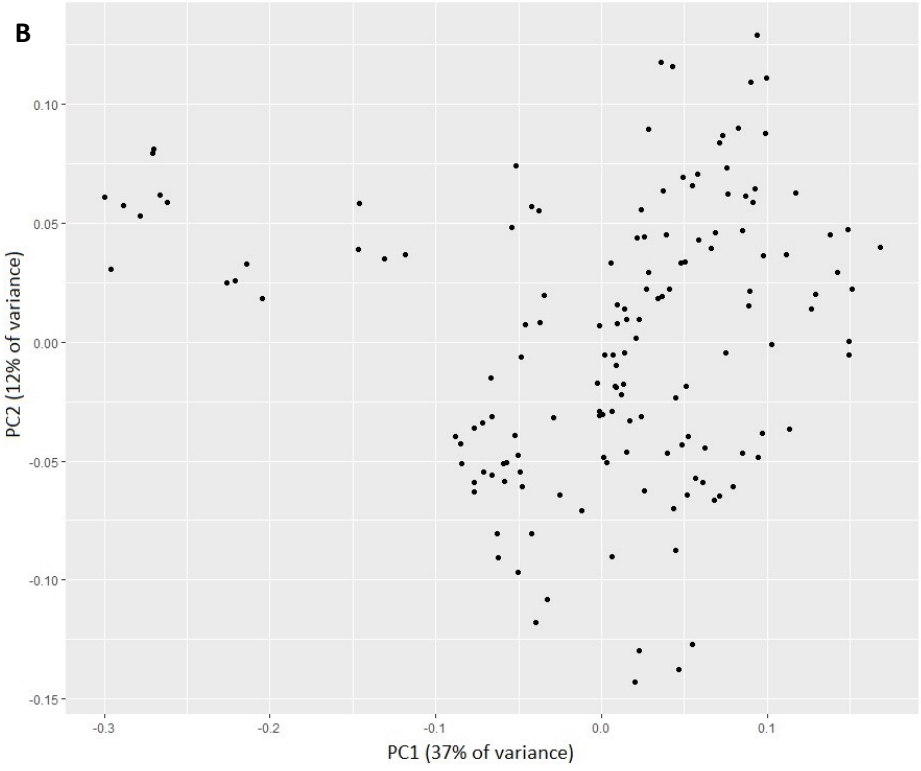

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3 Figure 3: Results of principal components analysis (PCA). (A) proportion of variance for each principal

4 component, while (B) PC1 (37% of variance) and PC2 (12% of variance) scores of each specimen.

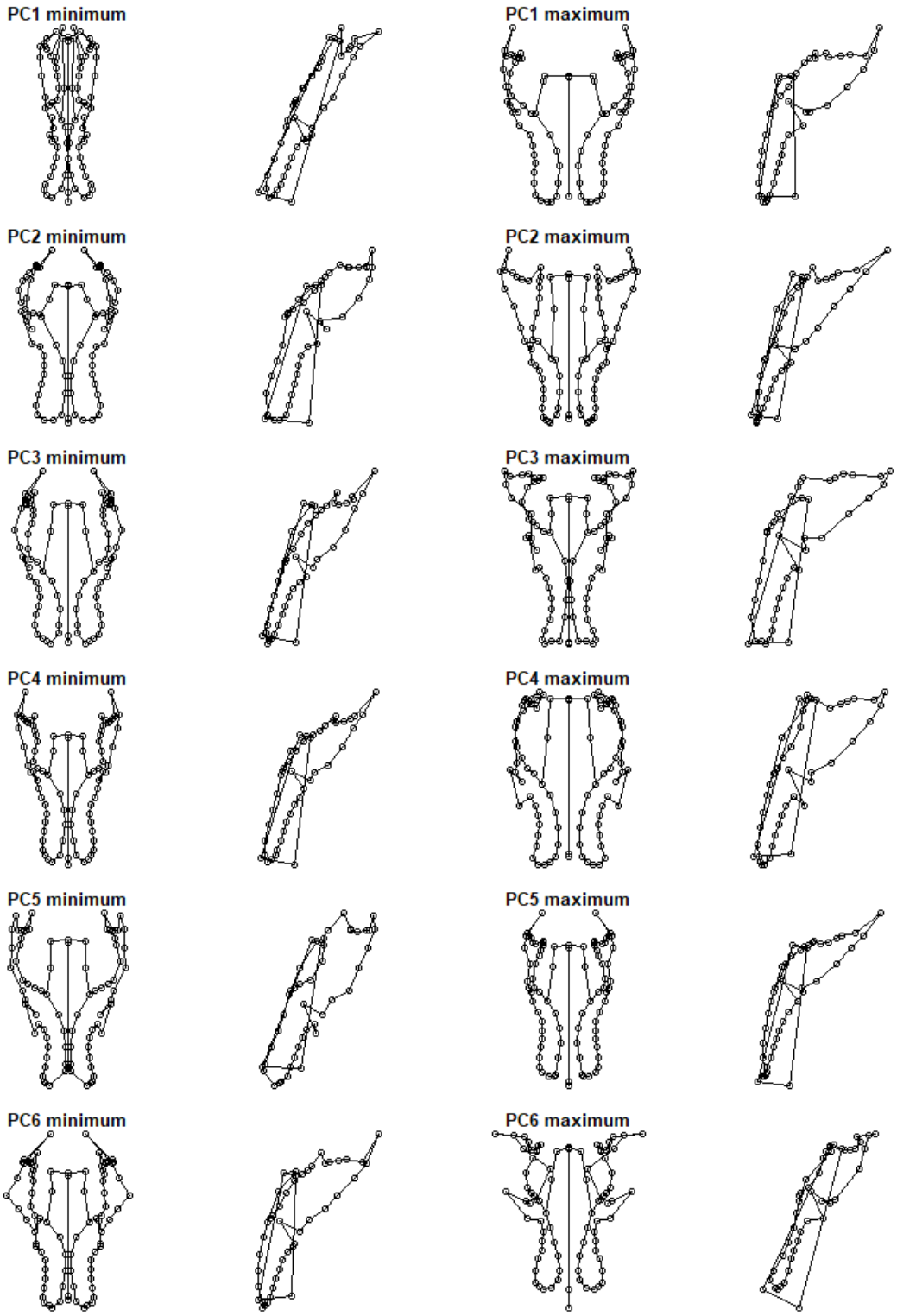

Figure 4: Maximum and minimum scoring shape configurations for each of the first six principal components. To ensure a consistent view from the 3D plots, the antitrochanter landmarks were superimposed in lateral view, and the posterior synsacral landmarks were superimposed in dorsal view.

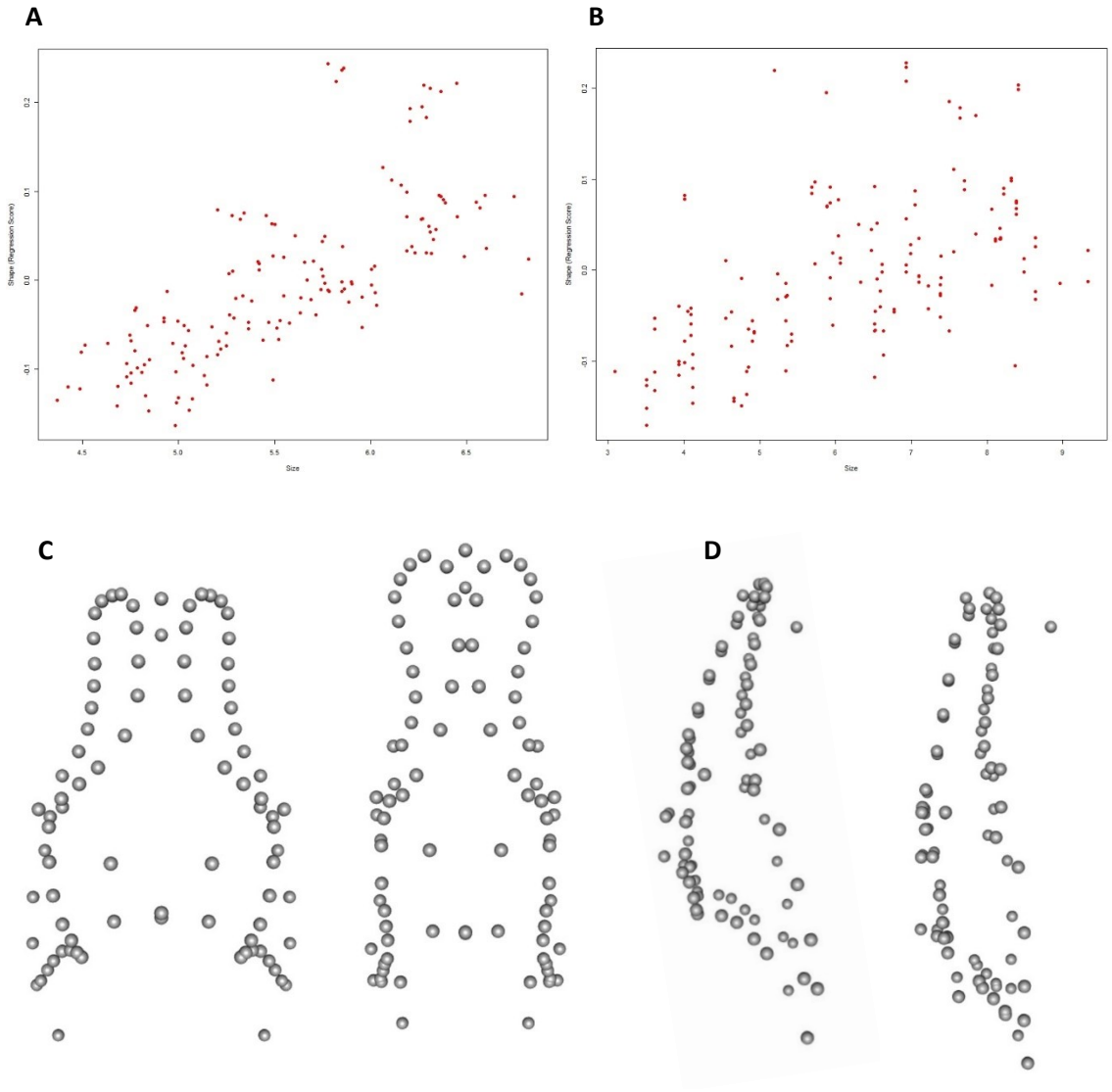

Figure 5: Plots of shape (Procrustes regression score) against size for (A) centroid size and (B) mass. Also shown are the minimum (left) and maximum (right) scoring shape configurations in dorsal (C) and lateral (D) view.

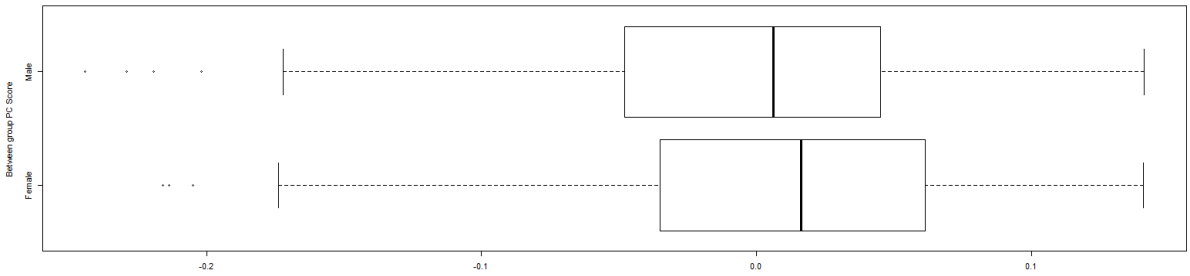

Figure 6: Box plots of between-group principal component scores for male and female specimens.

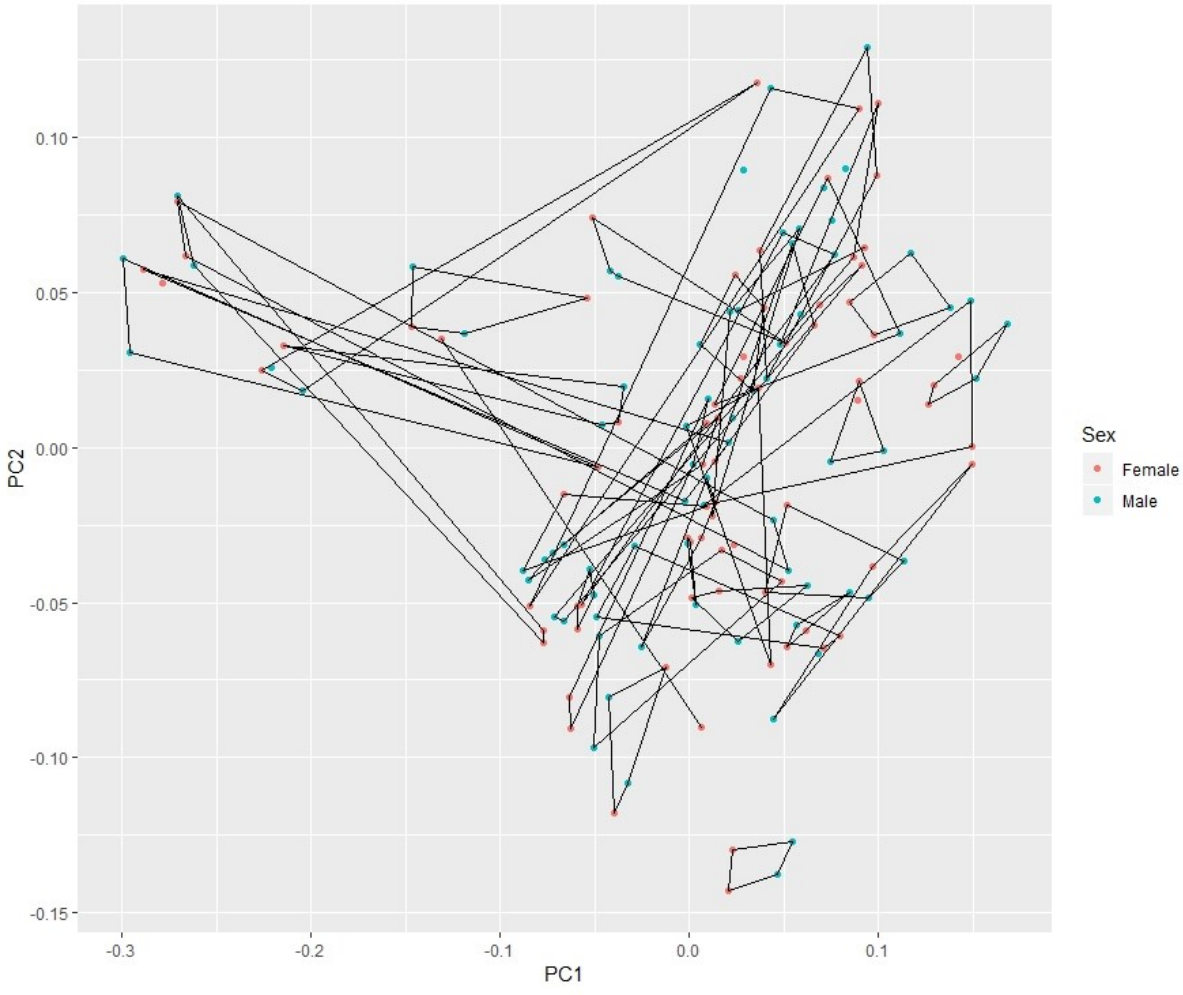

Figure 7: Plot of PC1 against PC2 for all specimens, with specimens coloured according to sex and with convex hulls outlining specimens of each taxon to allow visualisation of species shape patterns.

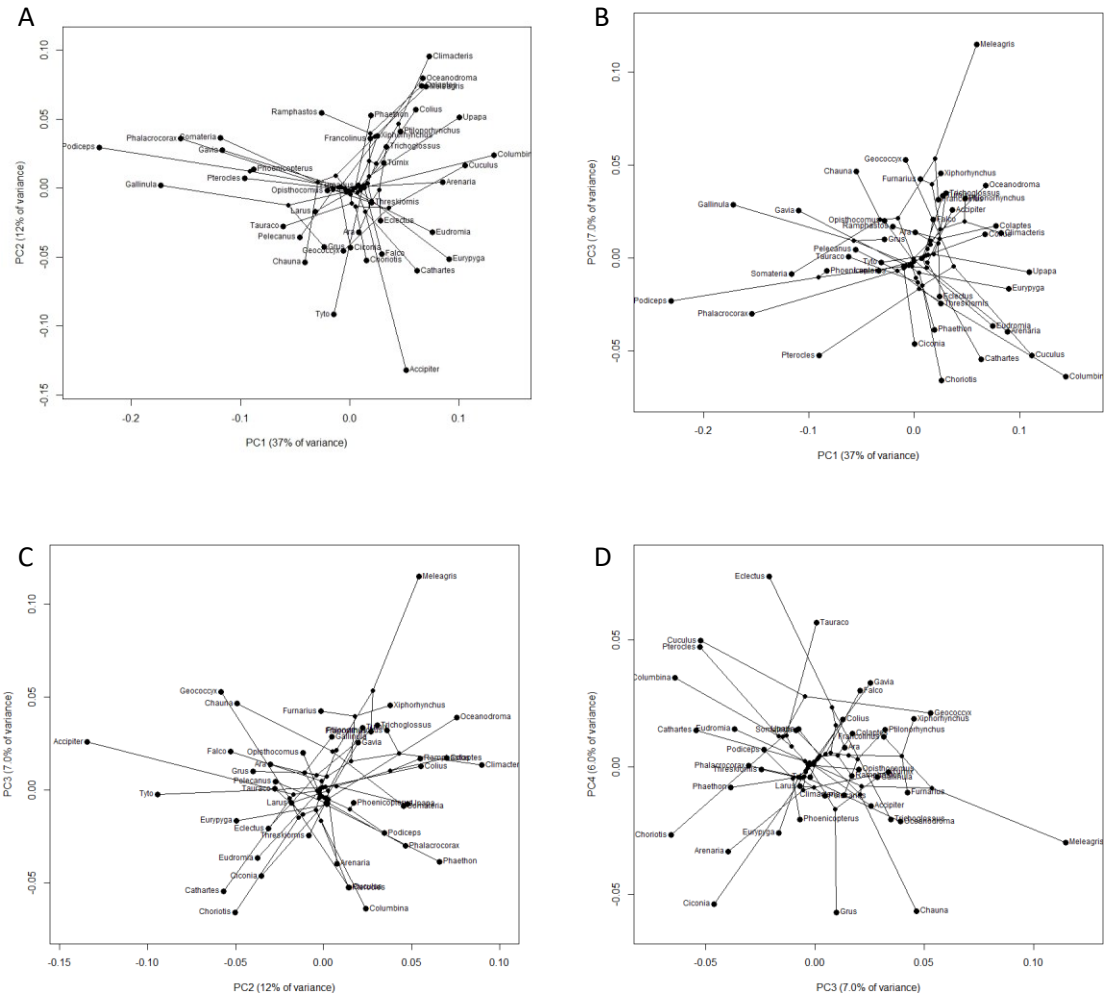

Figure 8: Phylomorphospace showing phylogeny plotted against principal components. (A) PC1 and PC2, (B) PC1 and PC3 (C) PC2 and PC3 (D) PC3 and PC4. Average PC scores for each genus are shown.

When the PC scores are visualised (Figure 9), it can be seen that the carnivores, in particular, seem to have a distinctive separation from the other hindlimb functional groups. The phylogenetic and nested MANOVAs (Table 3) confirm at least one significant difference among means of functional groups ($p = 0.0008$ and $p = 0.0005$, respectively). The exploration of this using the pairwise Hotelling's T^2 tests (Table 4) confirms the visual separation of the carnivores from other functional groups, but also shows a number of other significant separations in shape space. Divers and walkers are both significantly different from all other functional groups, excepting the paddlers. The paddlers are only significantly different from the carnivores, suggesting that the paddlers overlap substantially with other functional groups. Perchers and climbers also do not show a significant difference in mean.

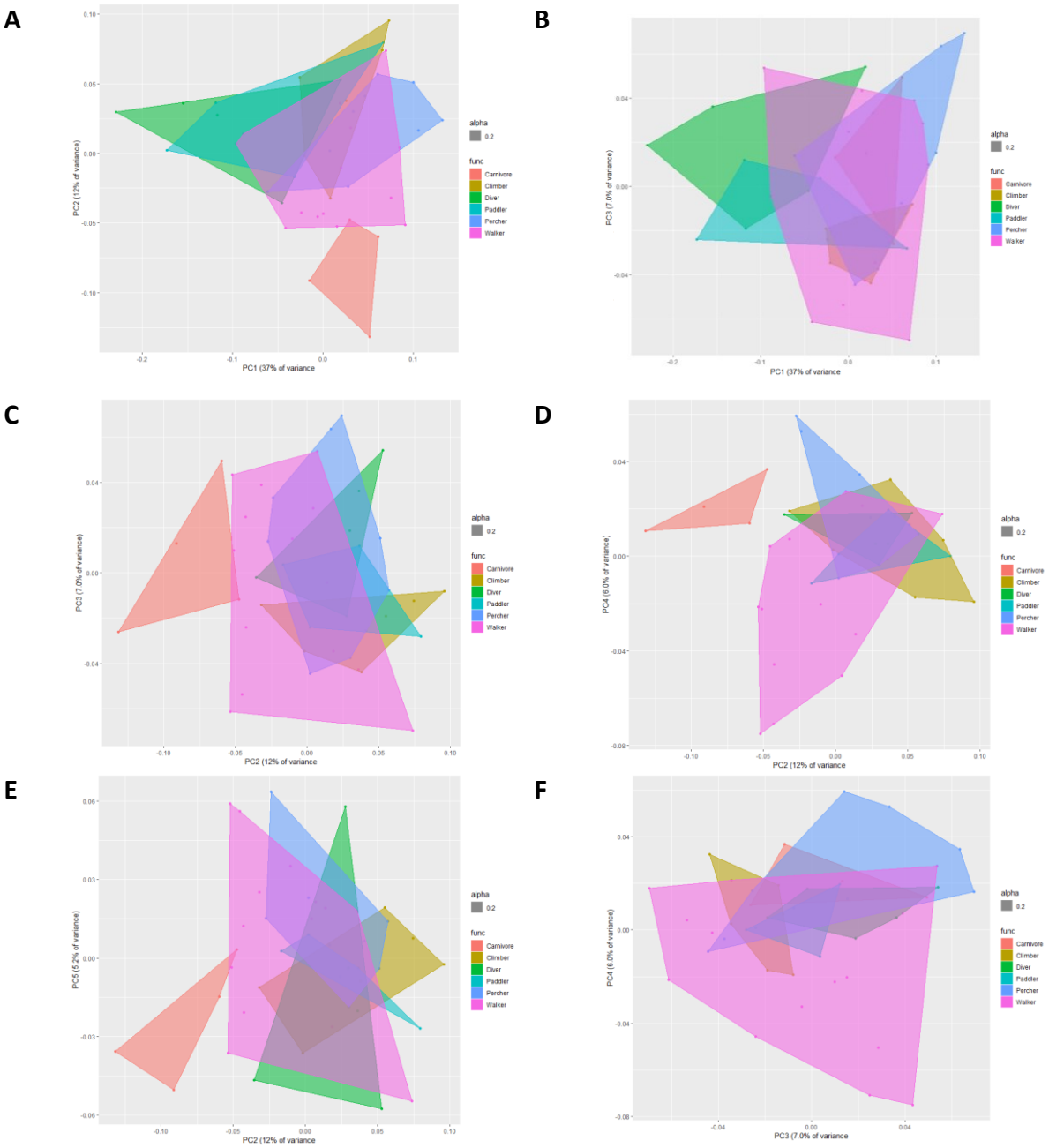

Figure 9: Principal component plots for some of the major PC axes. Polygons are coloured according to hindlimb function category to allow visualisation of separation and overlap of groups in projections of shape space.

Non phylogenetic				
	Degrees of freedom	Approximate F value	*p*	-
Function	5	2.03	0.000513	
Residuals	36			
Phylogenetic				
	Degrees of freedom	Approximate F value	*p*	*p* given phylogeny
Function	5	2.11	0.000803	0.000799
Residuals	36			

Table 3: MANOVA results of principal component scores, using hind-limb functional group as a factor. Non-phylogenetic MANOVA uses specimens in genus as a random nested variable, while the phylogenetic MANOVA uses the average PC score for each species.

	Carnivore	Climber	Diver	Paddler	Percher	Walker
Carnivore	-	T^2=65.3 p=8 x 10^{-7}	T^2=27.9 p=8 x 10^{-6}	T^2=33.1 p=5 x 10^{-4}	T^2=15.3 p=2 x 10^{-8}	T^2=6.55 p=1 x 10^{-7}
Climber		-	T^2=33.3 p=1 x 10^{-7}	T^2=5.84 p=0.007017	T^2=1.95 p=0.05547	T^2=4.98 p=3 x 10^{-6}
Diver			-	T^2=2.88 p=0.05045	T^2=6.85 p=5 x 10^{-6}	T^2=5.20 p=1 x 10^{-6}
Paddler				-	T^2=2.69 p=0.01315	T^2=2.55 p=0.004305
Percher					-	T^2=5.06 p=3 x 10^{-7}
Walker						-

Table 4: Results of pairwise Hotelling's T^2 test between functional hindlimb groups. Scores significant below the Bonferroni adjusted significance level of 0.0033 are shaded grey, both above and below the diagonal to allow ease of interpretation.

Conclusions and discussion

That body size and pelvic shape show a significant relationship was not particularly surprising, as many similar studies have analysed aspects of bird biology and found a functional allometric effect on performance or life history (Maloiy et al. 1979, Møller 1988, Brooke et al. 1999, Alerstam et al. 2007), however the weakness of the correlation between the two was surprising. Those studies that have looked at the limbs have often looked at adaptations to flightlessness (Maloiy et al. 1979, Alexander 1983, Picasso 2012) or other locomotor effects (Doube et al. 2012, Stoessel et al. 2013, Anten-Houston et al. 2017). This study, like those, finds that body mass has a significant effect on the morphology of the hindlimb, although with a weak predictive power. This previous research (Hertel et al. 2007, Stoessel et al. 2013, Anten-Houston et al. 2017) finds that increasing size appears to lead to increase in sizes of muscular surface area attachments, or of supportive bone contact surface areas (Hertel et al. 2007). With mass scaling to the cube of length, it is not surprising that we see a disproportionate increase in those parts of the skeleton. The elongate shape found in the larger pelves of this study (Figure 5) would provide an increased surface area for the attachment of the hip musculature, and so it could be speculated that a pelvis exhibiting this morphology could provide greater locomotor forces to the hind-limb, while not increasing the width, and therefore mass, of the trunk. When regressed against the logarithmically transformed measures of body size, individual PCs generally did not show significant relationships. An exception to this was PCs 1 and 2, which correlated negatively, though weakly, with centroid size (PC1: slope = -0.099, $R^2 = 0.35$, $p = 1x10^{-15}$; PC2: slope = -0.0.39, $R^2 = 0.16$, $p = 2x10^{-7}$) and body mass (PC1: slope = -0.026, $R^2 = 0.16$, $p = 2x10^{-7}$; PC2: slope = -0.012, $R^2 = 0.11$, $p = 2$ x

10^{-5}). As can be seen in Figure 4, lower scores along PC1 describe a more elongate pelvis, while lower scores along PC2 describe an expanded preacetabular process of the ilium and an ischium, both key sites for muscular attachment for the lower limb (George & Berger, 1966). A similar result was discussed in Anten-Houston et al. (2017), which finds that measurements of pelvic width are isometric to body mass, but that pelvic length measures scale with positive allometry. Such a trend would act to minimise mass gain with increasing size, by not scaling all dimensions of the bird equally. It would also serve to provide, as Anten-Houston et al. (2017) observe, extra surface area to the pelvis for muscle attachment. This would assist in producing the disproportionately increased locomotor forces that would be required to move a bird of increased size, not only during non-aerial locomotion, but also during launch and landing of volant taxa.

It must be considered that body size and function are not entirely independent of each other, with some functional groups being, on average, larger than others. Some attempt was made to mitigate this by choosing a selection of body sizes in all functional groups, however the effect was not eliminated as the heaviest group (Walkers, weighted mean mass 2485g) were an order of magnitude more massive than the lightest (Perchers, weighted mean mass 119g). However, when we consider functional groups with broadly similar mean masses (walkers at 2485g and divers at 2430g, and carnivores at 909g and paddlers at 879g) we see that they still have significant differences in morphology (Table 4). In fact, the only group that paddlers were significantly different in shape from were the comparably sized carnivores. Climbers, with a mean mass of 455g, were smaller in size, almost halfway between perchers and paddlers, yet these were the only two

functional groups that the climbers did not have a significantly different morphology from. It therefore seems that the relationship between body size and pelvic morphology is at best weak, and potentially localised to smaller subclades of birds.

By contrast, the results for sexual dimorphism across birds as a whole do seem to contrast with the previous literature. Many studies of sexual dimorphism have been undertaken (Reynolds 1972, Schnell et al. 1985, Temeles 1985, Olsen & Olsen 1987, Winker et al. 1994, Green 2000, Badyaev et al. 2000, Székely et al. 2000, Helfenstein et al. 2004, Bavoux et al. 2006, Svagelj & Quintana 2007, Székely et al. 2007, Shatkovska et al. 2018) and show that both in size and in shape, male and female birds differ. These differences are suggested to be due to a number of causes, from energetics (Reynolds 1972), to reproductive strategy (Shatkovska et al. 2018), to prey interactions (Olsen & Olsen 1987). However, these studies tend to be on smaller taxonomic groupings, to evaluate multiple regions of the skeleton and tend to have larger sample sizes of males and female from each species. In many cases, they are designed to allow categorisation of sex in species where this is otherwise difficult (Schnell et al. 1985, Svagelj & Quintana 2007).

These results show that, at this taxonomic level, consistent shape differences between males and females (Figures 6 & 7) are at most contributing only a small amount to total shape variance, with variation in shape among species contributing much more. Nor is there a significant size trend between males and females when birds are considered as a whole. This dataset has not been designed to look explicitly at sexual dimorphism, but

this result suggests that any further analysis of dimorphism would need to be focussed on sub-clades within birds and would need substantially higher sample sizes for each sex to allow a pattern to be identified.

When projected into phylomorphospace (Figure 8), the tree appears to remain clustered in its central portion in more basal nodes, and to project out rapidly nearer the tips. This suggests that even fairly closely related taxa can have quite different morphologies and suggests rapid morphological divergence. This must, however, be interpreted with caution, as visual inspection of tree topology (Figure 2) shows that the basal branch lengths of this tree are substantially shorter than those at the tips. This pattern is common in many phylogenies and is hypothesised to represent rapid diversification in birds after the end-Cretaceous mass extinction (Brusatte et al. 2015). The presence of fossil-calibration in the tree of Prum et al. (2015) helps to reassure that this is a true pattern, rather than a molecular clock artefact. Furthermore, selection for this dataset removed a large number of the taxa that are present in the full analysis by Prum et al. (2015) and further exacerbates this appearance of long branches. While it is possible that the removed taxa hide trends, breaking up the longer branches nearer the tips could constrain the topology of the tree in such a way as to require even faster morphological changes.

The significant results from both the phylogenetic and non-phylogenetic MANOVA (Table 3) confirm that at least some of the groups have significantly different means, and this is further supported by the pairwise Hotelling's T^2 tests (Table 4). The similarity between phylogenetic and non-phylogenetic results further suggests that phylogenetic

constraint seems relatively weak at the levels being analysed here, and suggests that a combination of body size and hind-limb function are stronger determinants of pelvic morphology in birds. As studies have considered previously (Reynolds 1972), these factors are not independent and are likely to interact. The ability to subdue prey would seem to require a larger body size, while the energetic cost of a larger body might select for a smaller one.

The pairwise Hotelling's T^2 tests (Table 4) confirm that carnivores at least are significantly separated from the other hindlimb function groups. This result was somewhat surprising, as it suggests that raptorial food processing with the hind-limb has a strong morphological signal. Divers too were significantly different from many of the other groups, with only paddlers not having a significantly different mean, which could infer an "aquatic" morphology. However, paddlers did not have a significantly different mean from any group except the carnivores. This may represent them as generalists, but it also bears consideration that the ecological habits of paddlers, foot-propelled divers and waders are somewhat overlapping themselves. Gulls, for example, cannot perch, but may be spotted wading, foraging terrestrially or swimming on the surface of the water.

Carnivores were found to have dorso-ventrally deep, medio-laterally wide and antero-posteriorly short pelves, with an overall equant aspect ratio. The post-acetabular half of the pelvis is mediolaterally broad relative to the pre-acetabular half, and the ischiadic surface is large. The pubes are slender and short, not extending substantially past the ischium posteriorly. This configuration would offer large surface areas for hip retractor

musculature and for musculature of the tail generally (George & Berger 1966). Strong retractors of the hip may be useful in feeding due to the need to pin the food down to the ground in order to allow the beak to tear away meat, while larger tail musculature may contribute to greater aerial maneuvrability, though the tail has not been the focus of this study.

Climbing birds tended to have the post-acetabular part of the ilium medio-laterally wide, with a moderately large pre-acetabular ilium and a moderate dorso-ventral depth. However, they do exhibit a lateral flaring of the ischium and pubis. This arrangement may potentially allow a greater range of joint excursions for mobility, rotating the acetabulae to allow the feet to contact the substrate further apart from each other, increasing the potential reach for grasping, or giving a more stable base. The ischium is relatively large, and the pubis elongate, also giving a large surface area for retractor musculature (George & Berger 1966), potentially allowing retraction of the femur against gravity.

In general, diving birds have antero-posteriorly elongate, medio-laterally narrow and dorso-ventrally shallow pelves, with the distal pubes flared and medially directed, and with very small pre-acetabular portions of the ilia. However, they occupy a larger range of morphospace than the carnivores, so this definition is slightly more flexible. This elongation may be a result of a more hydrodynamic general body form, as the surface area for muscle attachment of such a form is generally less, although with potentially greater moment arms.

The paddlers had a large area of morphospace covered, and in some components overlap substantially with other functional groups. They tend to a slightly more antero-posteriorly elongate form, but with a laterally flaring morphology of the ischium and pubis. Otherwise, on average they tended to be relatively unremarkable in morphology, possibly due to the wide range of morphospace they occupied, and suggesting that this group may benefit from further exploration. This generally unremarkable morphology was a surprise, as I had anticipated that paddling birds would exhibit more of the elongate shape found in the diving birds. The lateral flaring of the ischium in this instance may act to rotate the acetabulum and bring the feet laterally in order that the webbed toes generally possessed by this group may clear each other during the swimming stroke.

On average, perchers tended to have relatively equant pelves, with relatively large pre-acetabular ilia, making a large surface area available to musculature of hip protraction. They also often had relatively straight, relatively short pubes, fairly dorsoventrally shallow ischia and relatively medio-laterally wide sacra. As perchers have the smallest average mass and frequently use a digital tendon locking mechanism to passively flex the digits for perching (Quinn & Baumel 1990), they are most likely to use a protracted hip position, potentially explaining the relatively high surface area available for the attachment of hip protractors in this functional group.

The walkers seem to occupy the largest area of morphospace and overlap extensively with the other functional groups (Figure 9). They do not occupy the elongate morphospace of the divers, but otherwise they occupy large proportions of the total

morphospace available and therefore have a relatively unremarkable average shape. This may reflect the fact that all birds must be able to utilise the ground to some extent, for example following falls, while drinking or while learning to fly. Alternatively, it may represent a group in which less common but more functionally demanding behaviours dominate the morphology of the pelvis, and these species may therefore occupy the morphospace of the functional group that they share a hind-limb function with. In other groups, phylogenetic constraints would make a plausible explanation for such a pattern. While a phylogenetic constraint cannot be ruled out here, the general pattern of morphological lability this work suggests would be an argument against it. Overall, further analysis at a finer taxonomic and functional level, similar to the analyses of Ibáñez & Tambussi (2012) and Bell et al. (2019) seems likely to produce better resolution across all functional groups.

These results are consistent with other studies that have found significant differences in multivariate hindlimb morphology between locomotor groups in birds (Bell & Chiappe 2011, Ibáñez & Tambussi 2012, Anten-Housten et al. 2017, Bell et al. 2019), although it is the first to address the pelvis itself using three-dimensional landmarks and has one of the largest taxonomic coverages so far analysed.

The hind-limb functional groups analysed here are comparable to those of previous studies at large taxonomic scale (Bell & Chiappe 2011, Anten-Houston et al. 2017), though they do not use categories as narrow as some of the studies on smaller taxa (Ibáñez & Tambussi 2012, Bell et al. 2019). This is due to the larger sample sizes that

would be required to study avian pelvic morphology as a whole with such narrow classifications, though such study may prove fruitful.

Hypothesis 1: Birds will exhibit significant clustering in morphospace between hindlimb functional groups.

This hypothesis is supported with carnivores occupying a region of morphospace distinct to all other groups, and divers being distinct from all groups except paddlers.

Hypothesis 2: Some aspects of pelvic shape change will be better explained by body size than hindlimb function.

This hypothesis is not supported, with pelvic shape being only weakly correlated to body size in birds.

Hypothesis 3: When phylogenetic relationships are accounted for, hindlimb functional groups will remain more similar than phylogenetic groups.

This hypothesis is supported: even when phylogeny was taken into account, the PC scores of functional groups were still significantly different.

Birds appear to show that pelvic morphology is responsive to hind-limb function, rather than being constrained phylogenetically. They show a significant, though weakly correlated relationship between shape and body size. They show significantly different pelvic morphologies between hind-limb functional groups, and the differences between those groups do not become non-significant when phylogeny is taken into account.

This pattern likely reflects the separation of locomotor modules in birds, with birds generally utilising the fore-limb solely for flight and the hind-limb almost exclusively for non-aerial locomotion (Gatesy & Dial 1996). Although the tail remains part of the flight module (with its musculature anchored onto the pelvis) and the hind-limbs obviously contribute to launch and landing in flighted taxa, the phylogenetically independent morphological grouping of different hind-limb functions suggests that in birds hind-limb function is a strong controlling factor in pelvic morphology. This suggests that pelvic morphology of birds is relatively labile, especially as disparate phylogenetic lineages plot together in morphospace (e.g. the carnivores *Falco, Accipiter, Tyto* and *Cathartes*).

The specific grouping of the carnivores supports research by Struble & Organ (2016) that argues for a distinctive raptorial "footing" style, where the primary tool for manipulation of objects are the feet, rather than the beak. The results are also consistent with other morphometric analyses on the pelvis, with the geometric morphometric analysis of Ibáñez & Tambussi (2012) most directly comparable, which also found a relationship between hindlimb function and pelvic morphology. However, studies that focussed on the entire hind-limb showed conflicting results. Stoessel et al. (2013) reported that the mixed function of the hindlimb in birds obscured ecological signal, but Anten-Houston et al. (2017) and Bell et al. (2019) reported functionally significant relationships between general morphometric measures of the hind-limb and locomotor style.

Given the common use of relationships between ecology and morphology in extant birds to infer ecology in extinct taxa (Hinić-Frlog & Motani 2010, Anten-Houston et al. 2017, Deeming & Mayr 2018, Bell et al. 2019), these results add validity to this practice and suggest that non-aerial locomotor ecology may be able to be inferred from pelvic morphology in a wider sample of species, rather than just the extinct water birds that have been focussed on so far.

The lack of a consistent direction of sexual dimorphism in avian species was somewhat surprising, as it would seem probable that females would tend to possess a medio-laterally wider pelvis to allow for the passage of eggs, although this study was not designed to test for this extensively, and samples of males and females were small, and so further research would need to be done. The passage of eggs has been put forward as a key constraint that had to be removed to allow for the relatively large, round and equant eggs of modern birds when compared to those of non-avian dinosaurs (Varricchio & Jackson 2016). Dyke & Kaiser (2010) propose that the lack of a ventral pelvic symphysis in birds was the innovation that relaxed that constraint. However, the pelvis is still shown to correlate with egg size and shape in extant birds (Endo et al. 2012, Shatkovska et al. 2018) demonstrating that this constraint is not entirely removed and may be conflated with reproductive constraints on egg size (e.g. offspring fitness; Krist 2011).

In summary, this work suggests that non-volant functional requirements may be more important to construction of the avian pelvis than reproductive or flight requirements. This lends weight to work being undertaken to reconstruct functional ecology from the

avian pelvis, and suggests that exploration of pelvic morphology in other taxa might also be informative of function.

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1 Appendix 1

Taxon	ID	Specimen no. (USNM)	Nearest relation in Prum et al. (2015)	Shared level	Family	Family reference	Order	Mass (g)	Hindlimb function	Function reference
Accipiter gentilis	F1	322687	*Accipiter superciliosus*	Genus	Accipitridae	Prum et al. 2015	Accipitriformes	1089	Carnivore	Erlich et al. 1988
	F2	499642	*Accipiter superciliosus*	Genus	Accipitridae	Prum et al. 2015	Accipitriformes	1089	Carnivore	Erlich et al. 1988
	M1	322685	*Accipiter superciliosus*	Genus	Accipitridae	Prum et al. 2015	Accipitriformes	749	Carnivore	Erlich et al. 1988
	M2	610741	*Accipiter superciliosus*	Genus	Accipitridae	Prum et al. 2015	Accipitriformes	749	Carnivore	Erlich et al. 1988
Ara chloropterus	F1	345850	*Deroptyus*	Family	Psittacidae	Wright et al. 2008	Psittaciformes	1214	Climber	Cornell Ornithology Laboratory
	F2	490125	*Deroptyus*	Family	Psittacidae	Wright et al. 2008	Psittaciformes	1214	Climber	Cornell Ornithology Laboratory
	M1	623234	*Deroptyus*	Family	Psittacidae	Wright et al. 2008	Psittaciformes	1214	Climber	Cornell Ornithology Laboratory
	M2	226876	*Deroptyus*	Family	Psittacidae	Wright et al. 2008	Psittaciformes	1214	Climber	Cornell Ornithology Laboratory
Arenaria interpres	F1	500787	-	-	Scolopacidae	Prum et al. 2015	Aequorlitornithes	138	Walker	Erlich et al. 1988
	F2	500723	-	-	Scolopacidae	Prum et al. 2015	Aequorlitornithes	138	Walker	Erlich et al. 1988
	M1	498433	-	-	Scolopacidae	Prum et al. 2015	Aequorlitornithes	134	Walker	Erlich et al. 1988
	M2	498381	-	-	Scolopacidae	Prum et al. 2015	Aequorlitornithes	134	Walker	Erlich et al. 1988
Cathartes aura	F1	610725	*Cathartes burrovianus*	Genus	Cathartidae	Prum et al. 2015	Accipitriformes	1611	Carnivore	Erlich et al. 1988
	F2	610726	*Cathartes burrovianus*	Genus	Cathartidae	Prum et al. 2015	Accipitriformes	1611	Carnivore	Erlich et al. 1988
	M1	562524	*Cathartes burrovianus*	Genus	Cathartidae	Prum et al. 2015	Accipitriformes	1611	Carnivore	Erlich et al. 1988
	M2	490864	*Cathartes burrovianus*	Genus	Cathartidae	Prum et al. 2015	Accipitriformes	1611	Carnivore	Erlich et al. 1988
Chauna torquata	F1	614548	-	-	Anhimidae	Prum et al. 2015	Anseriformes	4400	Walker	Cornell Ornithology Laboratory
	F2	430022	-	-	Anhimidae	Prum et al. 2015	Anseriformes	4400	Walker	Cornell Ornithology Laboratory
	M1	614549	-	-	Anhimidae	Prum et al. 2015	Anseriformes	4400	Walker	Cornell Ornithology Laboratory
	M2	614547	-	-	Anhimidae	Prum et al. 2015	Anseriformes	4400	Walker	Cornell Ornithology Laboratory
Choriotis kori	F1	646638	-	-	Otididae	Prum et al. 2015	Otidimorpha	5635	Walker	Campbell & Lack, 1985
	F2	622453	-	-	Otididae	Prum et al. 2015	Otidimorpha	5635	Walker	Campbell & Lack, 1985
	M1	646640	-	-	Otididae	Prum et al. 2015	Otidimorpha	11281	Walker	Campbell & Lack, 1985

	M2	631759	-	-	Otididae	Prum et al. 2015	Otidimorpha	11281	Walker	Campbell & Lack, 1985
Ciconia ciconia	F1	605011	*Ciconia nigra*	Genus	Ciconiidae	Prum et al. 2015	Aequorlitornithes	3325	Walker	Campbell & Lack, 1985
	F2	605020	*Ciconia nigra*	Genus	Ciconiidae	Prum et al. 2015	Aequorlitornithes	3325	Walker	Campbell & Lack, 1985
	M1	291559	*Ciconia nigra*	Genus	Ciconiidae	Prum et al. 2015	Aequorlitornithes	3571	Walker	Campbell & Lack, 1985
	M2	289115	*Ciconia nigra*	Genus	Ciconiidae	Prum et al. 2015	Aequorlitornithes	3571	Walker	Campbell & Lack, 1985
Climacteris leucophaea	M1	612735	*Climacteris melanura*	Genus	Climacteridae	Prum et al. 2015	Passeriformes	22	Climber	Campbell & Lack, 1985
Colaptes auratus	F1	555621	*Picus*	Family	Picidae	Webb & Moore 2005	Coraciimorphae	125	Climber	Erlich et al. 1988
	F2	553937	*Picus*	Family	Picidae	Webb & Moore 2005	Coraciimorphae	125	Climber	Erlich et al. 1988
	M1	554428	*Picus*	Family	Picidae	Webb & Moore 2005	Coraciimorphae	128	Climber	Erlich et al. 1988
	M2	553936	*Picus*	Family	Picidae	Webb & Moore 2005	Coraciimorphae	128	Climber	Erlich et al. 1988
Colius striatus	F1	291096	*Colius colius/Colius indicus*	Genus	Coliidae	Prum et al. 2015	Coraciimorphae	51.1	Percher	Campbell & Lack, 1985
	F2	291097	*Colius colius/Colius indicus*	Genus	Coliidae	Prum et al. 2015	Coraciimorphae	51.1	Percher	Campbell & Lack, 1985
	M1	491986	*Colius colius/Colius indicus*	Genus	Coliidae	Prum et al. 2015	Coraciimorphae	51.1	Percher	Campbell & Lack, 1985
	M2	428106	*Colius colius/Colius indicus*	Genus	Coliidae	Prum et al. 2015	Coraciimorphae	51.1	Percher	Campbell & Lack, 1985
Columbina passerina	F1	555747	*Columbina minuta*	Genus	Columbidae	Prum et al. 2015	Columbimorphae	33.4	Perching	Erlich et al. 1988
	F2	554551	*Columbina minuta*	Genus	Columbidae	Prum et al. 2015	Columbimorphae	33.4	Perching	Erlich et al. 1988
	M1	555752	*Columbina minuta*	Genus	Columbidae	Prum et al. 2015	Columbimorphae	33.4	Perching	Erlich et al. 1988
	M2	554401	*Columbina minuta*	Genus	Columbidae	Prum et al. 2015	Columbimorphae	33.4	Perching	Erlich et al. 1988
Cuculus canorum	F1	603554	*Cuculus optatus*	Genus	Cuculidae	Prum et al. 2015	Otidimorpha	106	Percher	Campbell & Lack, 1985
	F2	603563	*Cuculus optatus*	Genus	Cuculidae	Prum et al. 2015	Otidimorpha	106	Percher	Campbell & Lack, 1985
	M1	552926	*Cuculus optatus*	Genus	Cuculidae	Prum et al. 2015	Otidimorpha	117	Percher	Campbell & Lack, 1985
	M2	430854	*Cuculus optatus*	Genus	Cuculidae	Prum et al. 2015	Otidimorpha	117	Percher	Campbell & Lack, 1985
Eclectus roratus	F1	557942	*Barnadius*	Family	Psittacidae	Wright et al. 2008	Psittaciformes	561	Percher	Heinsohn et al. 2005
Eudromia elegans	F1	227489	-	-	Tinamidae	Prum et al. 2015	Tinamiformes	729	Walker	Cornell Ornithology Laboratory

	F2	344966	-	-	Tinamidae	Prum et al. 2015	Tinamiformes	729	Walker	Cornell Ornithology Laboratory
	M1	344991	-	-	Tinamidae	Prum et al. 2015	Tinamiformes	678	Walker	Cornell Ornithology Laboratory
	M2	345096	-	-	Tinamidae	Prum et al. 2015	Tinamiformes	678	Walker	Cornell Ornithology Laboratory
Eurypyga helias	F1	492379	-	-	Eurypygidae	Prum et al. 2015	Aequorlitornithes	210	Walker	Howell & Webb, 1995
	F2	320276	-	-	Eurypygidae	Prum et al. 2015	Aequorlitornithes	210	Walker	Howell & Webb, 1995
	M1	637209	-	-	Eurypygidae	Prum et al. 2015	Aequorlitornithes	210	Walker	Howell & Webb, 1995
	M2	613747	-	-	Eurypygidae	Prum et al	Aequorlitornithes	210	Walker	Howell & Webb, 1995
Falco peregrinus	F1	489907	*Falco sparverius*	Genus	Falconidae	Prum et al. 2015	Falconiformes	873	Carnivore	Erlich et al. 1988
	F2	553232	*Falco sparverius*	Genus	Falconidae	Prum et al. 2015	Falconiformes	873	Carnivore	Erlich et al. 1988
	M1	491395	*Falco sparverius*	Genus	Falconidae	Prum et al. 2015	Falconiformes	649	Carnivore	Erlich et al. 1988
	M2	291186	*Falco sparverius*	Genus	Falconidae	Prum et al. 2015	Falconiformes	649	Carnivore	Erlich et al. 1988
Francolinus capensis	F1	558460	*Numida*	Family	Phasianidae	van Niekerk & Mandiwana-Neudani 2018	Galliformes	547	Walker	van Niekerk & Mandiwana-Neudani 2018
	M1	558452	*Numida*	Family	Phasianidae	van Niekerk & Mandiwana-Neudani 2018	Galliformes	758	Walker	van Niekerk & Mandiwana-Neudani 2018
	M2	558453	*Numida*	Family	Phasianidae	van Niekerk & Mandiwana-Neudani 2018	Galliformes	758	Walker	van Niekerk & Mandiwana-Neudani 2018
Furnarius leucopus	F1	632352	*Furnarius rufus*	Genus	Furnariidae	Prum et al. 2015	Passeriformes	54.8	Percher	Dyrcz 1987
	F2	500536	*Furnarius rufus*	Genus	Furnariidae	Prum et al. 2015	Passeriformes	54.8	Percher	Dyrcz 1987
	M1	500418	*Furnarius rufus*	Genus	Furnariidae	Prum et al. 2015	Passeriformes	54.8	Percher	Dyrcz 1987
	M2	500417	*Furnarius rufus*	Genus	Furnariidae	Prum et al. 2015	Passeriformes	54.8	Percher	Dyrcz 1987
Gallinula chloropus	F1	501118	*Porphyrio porphyrio*	Family	Rallidae	García-R et al. 2014	Gruiformes	294	Paddler	Erlich et al. 1988
	F2	347871	*Porphyrio porphyrio*	Family	Rallidae	García-R et al. 2014	Gruiformes	294	Paddler	Erlich et al. 1988
	M1	501117	*Porphyrio porphyrio*	Family	Rallidae	García-R et al. 2014	Gruiformes	359	Paddler	Erlich et al. 1988
	M2	318531	*Porphyrio porphyrio*	Family	Rallidae	García-R et al. 2014	Gruiformes	359	Paddler	Erlich et al. 1988
Gavia immer	F1	502465	-	-	Gaviidae	Prum et al. 2015	Aequorlitornithes	4500	Diver	Erlich et al. 1988

	F2	501601	-	-	Gaviidae	Prum et al. 2015	Aequorlitornithes	4500	Diver	Erlich et al. 1988
	M1	501599	-	-	Gaviidae	Prum et al. 2015	Aequorlitornithes	5640	Diver	Erlich et al. 1988
	M2	501598	-	-	Gaviidae	Prum et al. 2015	Aequorlitornithes	5640	Diver	Erlich et al. 1988
Geococcyx californianus	F1	501306	Sister to cuckoos excluding *Centropus*	Family	Cuculidae	Hughes 2000	Otidimorpha	376	Walker	Erlich et al. 1988
	F2	610962	Sister to cuckoos excluding *Centropus*	Family	Cuculidae	Hughes 2000	Otidimorpha	376	Walker	Erlich et al. 1988
	M1	621303	Sister to cuckoos excluding *Centropus*	Family	Cuculidae	Hughes 2000	Otidimorpha	376	Walker	Erlich et al. 1988
	M2	641953	Sister to cuckoos excluding *Centropus*	Family	Cuculidae	Hughes 2000	Otidimorpha	376	Walker	Erlich et al. 1988
Grus canadensis	F1	488555	-	-	Gruidae	Prum et al. 2015	Gruiformes	4096	Walker	Erlich et al. 1988
	F2	561056	-	-	Gruidae	Prum et al. 2015	Gruiformes	4096	Walker	Erlich et al. 1988
	M1	432705	-	-	Gruidae	Prum et al. 2015	Gruiformes	4848	Walker	Erlich et al. 1988
	M2	432500	-	-	Gruidae	Prum et al. 2015	Gruiformes	4848	Walker	Erlich et al. 1988
Larus argentatus	F1	488778	*Chroicocephalus cirrocephalus*	Family	Laridae	Pons et al. 2005	Aequorlitornithes	1022	Paddler	Erlich et al. 1988
	F2	488783	*Chroicocephalus cirrocephalus*	Family	Laridae	Pons et al. 2005	Aequorlitornithes	1022	Paddler	Erlich et al. 1988
	M1	636189	*Chroicocephalus cirrocephalus*	Family	Laridae	Pons et al. 2005	Aequorlitornithes	1150	Paddler	Erlich et al. 1988
	M2	612215	*Chroicocephalus cirrocephalus*	Family	Laridae	Pons et al. 2005	Aequorlitornithes	1150	Paddler	Erlich et al. 1988
Meleagris gallopavo	F1	556373	*Gallus gallus*	Family	Phasianidae	Guan et al. 2009	Galliformes	4300	Walker	Erlich et al. 1988
	M1	632170	*Gallus gallus*	Family	Phasianidae	Guan et al. 2009	Galliformes	7800	Walker	Erlich et al. 1988
Oceanodroma leucorhoa	F1	488200	-	-	Hydrobatidae	Prum et al. 2015	Aequorlitornithes	37	Paddler	Erlich et al. 1988
	F2	614217	-	-	Hydrobatidae	Prum et al. 2015	Aequorlitornithes	37	Paddler	Erlich et al. 1988
	M1	498223	-	-	Hydrobatidae	Prum et al. 2015	Aequorlitornithes	37	Paddler	Erlich et al. 1988
	M2	613267	-	-	Hydrobatidae	Prum et al. 2015	Aequorlitornithes	37	Paddler	Erlich et al. 1988
Opisthocomus hoatzin	F1	612024	-	-	Opisthocomidae	Prum et al. 2015	Opisthocomiiformes	696	Climber	Cornell Ornithology Laboratory
	M1	344066	-	-	Opisthocomidae	Prum et al. 2015	Opisthocomiiformes	696	Climber	Cornell Ornithology Laboratory
Pelecanus occidentalis	F1	553693	-	-	Pelecanidae	Prum et al. 2015	Aequorlitornithes	3174	Diver	Erlich et al. 1988

	F2	500863	-	-	Pelecanidae	Prum et al. 2015	Aequorlitornithes	3174	Diver	Erlich et al. 1988
	M1	553694	-	-	Pelecanidae	Prum et al. 2015	Aequorlitornithes	3702	Diver	Erlich et al. 1988
	M2	553695	-	-	Pelecanidae	Prum et al. 2015	Aequorlitornithes	3702	Diver	Erlich et al. 1988
Phaethon rubricauda	F1	498263	-	-	Phaethontidae	Prum et al. 2015	Aequorlitornithes	675	Diver	Howell & Webb, 1995
	F2	498355	-	-	Phaethontidae	Prum et al. 2015	Aequorlitornithes	675	Diver	Howell & Webb, 1995
	M1	621356	-	-	Phaethontidae	Prum et al. 2015	Aequorlitornithes	675	Diver	Howell & Webb, 1995
	M2	498356	-	-	Phaethontidae	Prum et al. 2015	Aequorlitornithes	675	Diver	Howell & Webb, 1995
Phalacrocorax auritus	F1	560560	*Phalacrocorax brasilianus*	Genus	Phalacrocoracidae	Prum et al. 2015	Aequorlitornithes	1808	Diver	Erlich et al. 1988
	F2	560585	*Phalacrocorax brasilianus*	Genus	Phalacrocoracidae	Prum et al. 2015	Aequorlitornithes	1808	Diver	Erlich et al. 1988
	M1	560264	*Phalacrocorax brasilianus*	Genus	Phalacrocoracidae	Prum et al. 2015	Aequorlitornithes	2077	Diver	Erlich et al. 1988
	M2	560561	*Phalacrocorax brasilianus*	Genus	Phalacrocoracidae	Prum et al. 2015	Aequorlitornithes	2077	Diver	Erlich et al. 1988
Phoenicopterus ruber	F1	558420	-	-	Phoenicopteridae	Prum et al. 2015	Aequorlitornithes	2573	Walker	Erlich et al. 1988
	F2	289740	-	-	Phoenicopteridae	Prum et al. 2015	Aequorlitornithes	2573	Walker	Erlich et al. 1988
	M1	223962	-	-	Phoenicopteridae	Prum et al. 2015	Aequorlitornithes	3529	Walker	Erlich et al. 1988
	M2	289736	-	-	Phoenicopteridae	Prum et al. 2015	Aequorlitornithes	3529	Walker	Erlich et al. 1988
Podiceps grisegena	F1	612774	*Rollandia rolland*	Family	Podicipedidae	Ogawa et al. 2015	Aequorlitornithes	1023	Diver	Erlich et al. 1988
	F2	612747	*Rollandia rolland*	Family	Podicipedidae	Ogawa et al. 2015	Aequorlitornithes	1023	Diver	Erlich et al. 1988
	M1	612778	*Rollandia rolland*	Family	Podicipedidae	Ogawa et al. 2015	Aequorlitornithes	1023	Diver	Erlich et al. 1988
	M2	612770	*Rollandia rolland*	Family	Podicipedidae	Ogawa et al. 2015	Aequorlitornithes	1023	Diver	Erlich et al. 1988
Pterocles decoratus	F1	636740	*Pterocles bicinctus*	Genus	Pteroclididae	Prum et al. 2015	Columbimorphae	180	Walker	Campbell & Lack, 1985
	M1	636739	*Pterocles bicinctus*	Genus	Pteroclididae	Prum et al. 2015	Columbimorphae	188	Walker	Campbell & Lack, 1985
	M2	636741	*Pterocles bicinctus*	Genus	Pteroclididae	Prum et al. 2015	Columbimorphae	188	Walker	Campbell & Lack, 1985
Ptilonorhynchus violaceus	F1	559121	-	-	Ptilonorhynchidae	Prum et al. 2015	Passeriformes	213	Percher	Campbell & Lack, 1985
	F2	612640	-	-	Ptilonorhynchidae	Prum et al. 2015	Passeriformes	213	Percher	Campbell & Lack, 1985

	M1	429869	-	-	Ptilonorhynchidae	Prum et al. 2015	Passeriformes	225	Percher	Campbell & Lack, 1985
	M2	620244	-	-	Ptilonorhynchidae	Prum et al. 2015	Passeriformes	225	Percher	Campbell & Lack, 1985
Ramphastos sulfuratus	F1	612339	*Ramphastos ambiguus*	Genus	Ramphastidae	Prum et al. 2015	Coraciimorphae	389	Climber	Howell & Webb, 1995
	F2	501337	*Ramphastos ambiguus*	Genus	Ramphastidae	Prum et al. 2015	Coraciimorphae	389	Climber	Howell & Webb, 1995
	M1	428078	*Ramphastos ambiguus*	Genus	Ramphastidae	Prum et al. 2015	Coraciimorphae	430	Climber	Howell & Webb, 1995
	M2	613424	*Ramphastos ambiguus*	Genus	Ramphastidae	Prum et al. 2015	Coraciimorphae	430	Climber	Howell & Webb, 1995
Somateria mollissima	F1	623302	*Aythya valisineria*	Family	Anatidae	Huang et al. 2016	Anseriformes	1915	Paddler	Erlich et al. 1988
	F2	632082	*Aythya valisineria*	Family	Anatidae	Huang et al. 2016	Anseriformes	1915	Paddler	Erlich et al. 1988
	M1	431988	*Aythya valisineria*	Family	Anatidae	Huang et al. 2016	Anseriformes	2218	Paddler	Erlich et al. 1988
	M2	36437	*Aythya valisineria*	Family	Anatidae	Huang et al. 2016	Anseriformes	2218	Paddler	Erlich et al. 1988
Tauraco corythaix	F1	636323	*Tauraco macrorhynchus*	Genus	Musophagidae	Prum et al. 2015	Otidimorpha	308	Percher	Campbell & Lack, 1985
	F2	636321	*Tauraco macrorhynchus*	Genus	Musophagidae	Prum et al. 2015	Otidimorpha	308	Percher	Campbell & Lack, 1985
Threskiornis aethiopicus	F1	558415	*Theristicus caerulescens*	Family	Threskiornithidae	Ramirez et al. 2013	Aequorlitornithes	1378	Walker	Campbell & Lack, 1985
	F2	558414	*Theristicus caerulescens*	Family	Threskiornithidae	Ramirez et al. 2013	Aequorlitornithes	1378	Walker	Campbell & Lack, 1985
	M1	620182	*Theristicus caerulescens*	Family	Threskiornithidae	Ramirez et al. 2013	Aequorlitornithes	1618	Walker	Campbell & Lack, 1985
	M2	430824	*Theristicus caerulescens*	Family	Threskiornithidae	Ramirez et al. 2013	Aequorlitornithes	1618	Walker	Campbell & Lack, 1985
Trichoglossus haematodus	F1	612676	*Barnadius*	Family	Psittacidae	Wright et al. 2008	Psittaciformes	95	Percher	Green et al. 1989
	F2	620215	*Barnadius*	Family	Psittacidae	Wright et al. 2008	Psittaciformes	95	Percher	Green et al. 1989
	M1	561570	*Barnadius*	Family	Psittacidae	Wright et al. 2008	Psittaciformes	102	Percher	Green et al. 1989
	M2	615014	*Barnadius*	Family	Psittacidae	Wright et al. 2008	Psittaciformes	102	Percher	Green et al. 1989
Turnix suscitator	F1	343205	*Turnix ocellatus*	Genus	Turnicidae	Prum et al. 2015	Aequorlitornithes	57.5	Walker	Campbell & Lack, 1985
Tyto alba	F1	491458	-	-	Tytonidae	Prum et al. 2015	Strigiformes	419	Carnivore	Erlich et al. 1988
	F2	500619	-	-	Tytonidae	Prum et al. 2015	Strigiformes	419	Carnivore	Erlich et al. 1988
	M1	610963	-	-	Tytonidae	Prum et al. 2015	Strigiformes	362	Carnivore	Erlich et al. 1988
	M2	553646	-	-	Tytonidae	Prum et al. 2015	Strigiformes	362	Carnivore	Erlich et al. 1988

Upapa epops	F1	603663	-	-	Upupidae	Prum et al. 2015	Coraciimorphae	61.4	Percher	Campbell & Lack, 1985
	F2	603635	-	-	Upupidae	Prum et al. 2015	Coraciimorphae	61.4	Percher	Campbell & Lack, 1985
	M1	603627	-	-	Upupidae	Prum et al. 2015	Coraciimorphae	61.4	Percher	Campbell & Lack, 1985
	M2	603658	-	-	Upupidae	Prum et al. 2015	Coraciimorphae	61.4	Percher	Campbell & Lack, 1985
Xiphorhynchus guttatus	F1	492323	*Furnarius rufus*	Infra-order	Dendrocolaptidae	Moyle et al. 2009, Rocha et al. 2015	Passeriformes	59.8	Climber	Howell & Webb, 1995
	F2	559353	*Furnarius rufus*	Infra-order	Dendrocolaptidae	Moyle et al. 2009, Rocha et al. 2015	Passeriformes	59.8	Climber	Howell & Webb, 1995
	M1	612353	*Furnarius rufus*	Infra-order	Dendrocolaptidae	Moyle et al. 2009, Rocha et al. 2015	Passeriformes	59.8	Climber	Howell & Webb, 1995
	M2	612352	*Furnarius rufus*	Infra-order	Dendrocolaptidae	Moyle et al. 2009, Rocha et al. 2015	Passeriformes	59.8	Climber	Howell & Webb, 1995

Appendix Table 1: Details of all specimens included in analysis, with references for relationships, mass and function.

CURRICULUM VITAE
The Johns Hopkins University School of Medicine

Rachel A. Frigot June 22nd 2019

Educational History

M.S. expected 2019		Program in Functional Anatomy and Evolution Mentors: Adam A. Sylvester, PhD and Christopher Ruff, PhD	Johns Hopkins School of Medicine
MSc	2012	Palaeobiology	University of Bristol
MSci	2009	Natural Sciences	University of Cambridge
BA(Hons)	2009	Natural Science	University of Cambridge

Scholarships

2012-2013 US-UK Fulbright Postgraduate Scholar, US-UK Fulbright Commission, stipend support $21,433

Student awards

2013 GSA Travel Award Graduate Student Association

Publications

Frigot, R. A. 2018. Pelvic musculature of *Vectidraco daisymorrisae* and consequences for pterosaur locomotion. In press. In: Hone, D; Witton, M. & Martill, D. (eds) *New Perspectives on Pterosaur Palaeobiology*. Geological Society, London, Special Publications 455, 45-55.

Benson, R. B. J.; **Frigot, R. A.**; Goswami, A.; Andres, B. & Butler, R. J. 2014. Competition and constraint drove Cope's rule in the evolution of giant flying reptiles. *Nature Communications* 5, 3567.

Posters and Abstracts

Frigot. R. A. 2016. Retroversion of the pubis in Pterosauria and its significance in reconstructing gait *Society of Vertebrate Paleontology Program and Abstracts Book*: 140A.

Frigot, R. A. 2015. The pterosaurian pelvis: An analytical view of morphological disparity and implications for locomotor evolution. *Society of Vertebrate Paleontology Program and Abstracts Book*: 127A.

Frigot, R. A. 2015. A geometric morphometric examination of form and function in the avian pelvis. *SVPCA & SPPC 2015, Abstract book*: 35.

Frigot, R. A. 2015. Pelvic musculature of *Vectidraco daisymorrisae*, biomechanical insights and a review of the field. *Flugsaurier 2015, International Symposium on Pterosaurs, Abstract book*: 22.

Frigot, R. A. and Palmer C. 2013. Biomechanical significance of trabecular architecture in pterosaurs. *Society of Vertebrate Paleontology Program and Abstracts Book*: 130A.
Frigot, R. A. and Palmer, C. 2013. Trabecular function in pterosaurs: insights from computer models. *Rio Ptero 2013 International Symposium on Pterosaurs, Short Communications*: 72.

Service and Leadership

2015-2016 Program Representative to the Graduate Student Association
2014-2016 Center Webmaster